

Poor downstream passage at a dam creates an ecological trap for migratory fish

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Abstract

Ecological traps can be caused when partial restoration leads organisms to make maladaptive habitat choices. One example of this is fishways (e.g., fish ladders) that provide upstream passage at dams but are not paired with adequate downstream passage. We tested the hypothesis that attracting anadromous fishes to spawn above a dam, but blocking downstream passage of their offspring leads to an ecological trap. Using passive integrated transponder (PIT) tags, we monitored the movements of steelhead (*Oncorhynchus mykiss*) at a dam and fishway on the central California coast. We found that downstream passage for juveniles and kelts was limited by four factors: migration delay, loss in the reservoir, avoidance of the downstream bypass, and water depths on the spillway. Based on the spillway-passage depth thresholds, we estimated that the ability for fish to pass downstream was limited to only half of the migration season in 55% of the past 20 years (2002–2021). Our results support the ecological trap hypothesis, which may explain why restoration using fishways has failed to produce recovery gains in this population and elsewhere.

Key words: ecological trap, fish passage, fishway, downstream passage, restoration, steelhead, dam

Résumé

Des pièges écologiques peuvent survenir quand une restauration partielle mène des organismes à faire des choix d'habitat mal adaptés. Des passes migratoires (p. ex., échelles à poissons) qui permettent le franchissement de barrages vers l'amont, mais qui ne sont pas jumelées à un passage adéquat vers l'aval en constituent un exemple. Nous avons validé l'hypothèse voulant que le fait d'attirer des poissons anadromes pour qu'ils fraient en amont d'un barrage tout en bloquant le passage vers l'aval de leur progéniture produise un piège écologique. Nous avons utilisé des étiquettes à transpondeur passif intégré (PIT) pour suivre les déplacements de saumons arc-en-ciel (*Oncorhynchus mykiss*) à travers un barrage et une passe migratoire dans le centre de la côte californienne. Nous avons constaté que le passage vers l'aval pour les juvéniles et les saumons vides est limité par quatre facteurs, soit les retards dans la migration, les pertes dans le réservoir, l'évitement du contournement vers l'aval et la profondeur de l'eau dans l'évacuateur. À la lumière des seuils de profondeur du passage dans l'évacuateur, nous estimons que, pour 55 % des 20 dernières années (2002–2021), les poissons ne pouvaient passer vers l'aval que durant la moitié de la période de migration. Nos résultats appuient l'hypothèse du piège écologique, ce qui pourrait expliquer pourquoi la restauration faisant appel à des passes migratoires n'a pas produit de gains dans le rétablissement de cette population et dans d'autres régions. [Traduit par la Rédaction]

Mots-clés : piège écologique, passage de poissons, passe migratoire, passage vers l'aval, restauration, saumon arc-en-ciel, barrage

Introduction

Ecological restoration is frequently undertaken with the goal of increasing abundances of target species by restoring the habitats in which those species live or reproduce (Palmer et al. 1997). Habitat restoration can be a complex task, and there are often many aspects of the habitat in need of repair

(Miller and Hobbs 2007). It may not be possible to fully restore all aspects of the habitat at once, so restoration is often undertaken in smaller, individual, parts (Gann et al. 2019). The conventional wisdom is that restoring some aspects of the habitat is better than no restoration (Palmer and Allan 2006; Gann et al. 2019). However, partial restoration comes

with risks, including the potential to leave populations even worse off by creating ecological traps.

Ecological traps occur when an organism makes a maladaptive habitat choice based on cues that previously indicated habitat quality (Schlaepfer et al. 2002; Robertson and Hutto 2006). Organisms often use cues from the physical environment to select habitats or time behaviors that will lead to better survival or reproductive success (e.g., Visser et al. 2010; Milner-Gulland et al. 2011). For example, juvenile salmon use high stream flows as a cue to start migrating to the ocean because migrating during high flows leads to higher survival (Quinn 2005). The ability to use certain cues is highly adaptive and is the product of natural selection (Williams and Nichols 1984). However, in environments that are altered by humans, a previously adaptive cue may lead to worse survival or reproductive success. For example, grassland birds select hay pastures for nesting based on previously adaptive cues for grasslands but experience high nestling mortality from hay harvesting (Schlaepfer et al. 2002). Ecological restoration can also create misleading cues, particularly if the restoration is incomplete. Incomplete, or partial, restoration has the potential to cause an ecological trap if it restores previously adaptive cues but does not lead to better survival or reproduction.

One widespread restoration technique with the potential to create ecological traps is engineered fish passage at dams (Pelicice and Agostinho 2008). Engineered fish passage is designed to reconnect riverways blocked by dams and is typically implemented through fishways that provide an upstream passage route (e.g., fish ladders, fish lifts, trap-and-haul, etc.; Bunt et al. 2012; Kock et al. 2021). Restoring upstream passage using fishways has been an especially common practice to improve conditions for anadromous fish populations (Silva et al. 2018). Anadromous fishes spawn in freshwater and migrate to the ocean as juveniles, so they are particularly susceptible to passage impediments at dams. Yet, despite the considerable investment in fishways, anadromous populations in dammed rivers have failed to recover, and in many cases, have continued to decline (Levin and Tolimieri 2001; McClure et al. 2003; Hall et al. 2012; Rand et al. 2012). One reason for the continued declines may be that fishways are creating ecological traps by attracting adults to spawn above dams, but failing to provide adequate downstream passage for out-migrating juveniles to reach the ocean.

Fishway restoration projects often make the assumption that juveniles are able to successfully pass downstream over the dam spillway or through power-generation turbines (Agostinho et al. 2011; Kock et al. 2019). However, the amount and seasonal timing of flow at the spillway or turbines varies by the purpose of the dam (e.g., power generation, flood control, drinking water), and may not match the outmigration season for some species (Keefer et al. 2013; Babin et al. 2020). There is also interannual variation in the amount of flow, and downstream passage can be severely limited in dry years (Ehsani et al. 2017). These variations in flow amount and timing could result in considerable interannual variability in the ability of fish to pass downstream. In addition, dams create reservoirs, which produce low-flow, limnetic conditions that can hinder fish from moving downstream

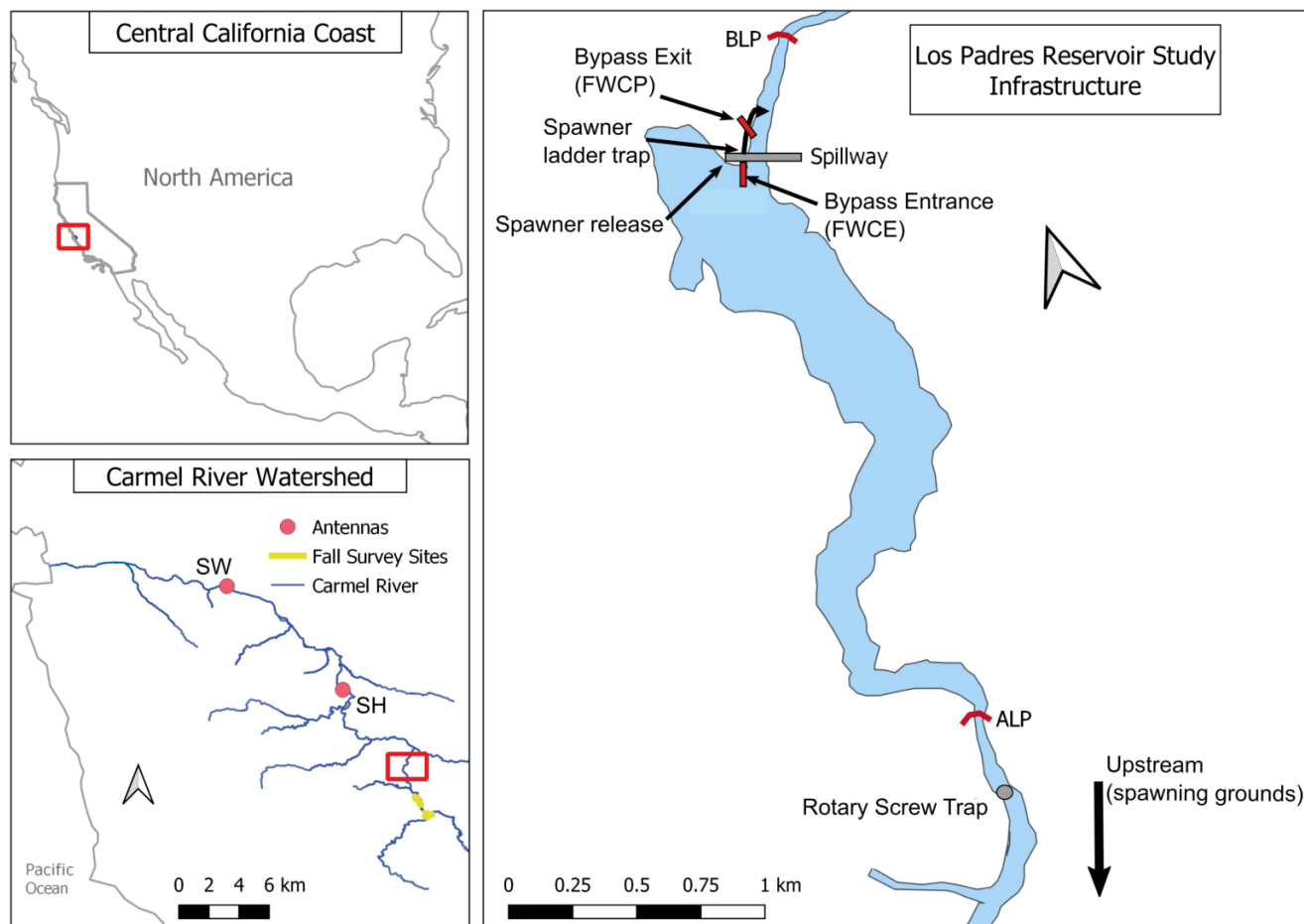
(Pelicice et al. 2015). Reservoirs can slow swimming speeds (Honkanen et al. 2018; Babin et al. 2020), delay migration as fish search for the outlet (Honkanen et al. 2021), and create conditions for high predation by providing habitat for non-native predators (Naughton et al. 2004) or advantageous conditions for native predators (Agostinho et al. 2007).

Inconsistent, or very limited, downstream passage at dams with fishways can therefore create ecological traps, which may explain why anadromous fish populations have not recovered in dammed watersheds, even after fishways have been installed (Pelicice and Agostinho 2008). However, despite the possibility for widespread ecological traps at dams with fishways globally, this phenomenon has only been studied on large Neotropical reservoirs (Pelicice and Agostinho 2008), and the adequacy of downstream passage at fishways is rarely evaluated outside of a few situations (e.g., the large dams on the well-studied Columbia and Snake rivers, USA; Skalski et al. 2021). In this study, we tested the hypothesis that fishways can create ecological traps by attracting adults to spawn above the dam but failing to successfully pass migrating juveniles and adults downstream. We used an extensive passive integrated transponder (PIT)-tagging study to track the movement rates of anadromous steelhead (*Oncorhynchus mykiss*) at a medium-sized dam and fishway on the Carmel River, on the central California coast. Steelhead at this dam pass upstream via a trap-and-haul fishway and can pass downstream either over the dam spillway or through a recently installed downstream bypass. Using this study system, we addressed the following specific questions: (1) Does the reservoir obstruct downstream passage by slowing migration speeds or preventing passage? (2) Do juvenile (i.e. parr and smolt) and adult (i.e., kelt) steelhead use the downstream bypass or the spillway for downstream passage? (3) Does water depth limit downstream passage via the spillway? (4) To what degree have water depths limited passage over the past 20 years? Our overall goal is to assess if successful upstream passage for steelhead adults, and poor downstream passage for juveniles and kelts has created the conditions for an ecological trap.

Methods

This study was conducted at the Los Padres dam on the Carmel River. The Carmel River watershed is 660 km² and experiences a Mediterranean climate that is mild and rainy in the winter and hot and dry in the summer, resulting in peak seasonal flows from winter to spring. Steelhead are native to the Carmel River and are the only anadromous salmonid in the watershed. The freshwater resident form of *Oncorhynchus mykiss* (rainbow trout) also occurs sympatrically in the watershed, but its relative abundance is unknown. Steelhead in California typically spend 1–2 years in freshwater as parr before smolting and return to spawn 1–2 years later (Busby et al. 1996). Smolts migrate to the ocean from March to June and spawners return from the ocean from December to May, both taking advantage of the high winter–spring flows. Some spawners die after spawning, whereas others survive and return to the ocean as kelts from February to June.

Fig. 1. Study site and PIT tag antenna locations for the Los Padres passage study. The Scarlett Well (SW) and Sleepy Hollow (SH) antenna sites are shown in the lower left. On the right, antenna sites Below Los Padres (BLP), downstream bypass pipe (FWCP) and downstream bypass floating weir collector entrance (FWCE), and Above Los Padres (ALP) are shown in red. Figure made by Karlee Liddy using the US coastline from Natural Earth, the California state boundary from data.ca.gov, and the Carmel Watershed from California Department of Fish and Wildlife's CalHydro 100k data set. Projection and coordinates in EPSG:3857. [Colour online.]



The Los Padres dam is located 42 river km (rkm) upstream of the ocean and creates a 2190 megalitre (ML) reservoir that is approximately 1.55 km long and 0.17 km wide (Fig. 1). At the base of the spillway, spawners can swim up a Denil-style fish ladder that leads to a large holding tank. They are then transported by truck to the top of the dam and released into the reservoir. The fish ladder is seasonally operated from December–June.

Juvenile outmigrants (parr or smolts) and kelts have two options for downstream passage. They can pass over the spillway, which is approximately 196-m long with a 9° slope. The spillway terminates in an 11.3 m drop into a plunge pool that is approximately 3-m deep. Fish can also pass downstream through a downstream bypass (hereinafter “bypass”), comprising a floating weir collector (FWC) and behavioral guidance system located adjacent to the spillway crest. The bypass was installed in 2016 and is a volitional passage system that is not augmented with attraction flows (HDR Engineering et al. 2021; Supplement A). The bypass was designed for juvenile, smolt, and kelt passage and is operational to reservoir

elevations 1.2 m below the spillway, which could provide passage opportunities even when the reservoir is too low to spill.

Capture and tagging methods

Juvenile outmigrants

We captured juvenile steelhead using two different methods. In the spring of 2019, we captured outmigrating juveniles and smolts in a rotary screw trap (RST) located upstream of the reservoir (Fig. 1). We operated the RST 4 days per week from March 1, 2019, to May 31, 2019, except for March 11, 2019, when operations ceased due to high flows. We also captured juvenile steelhead in 2017 and 2018 during fall surveys upstream of the reservoir. These fish were used to increase the sample size for estimating movement rates and speeds. Fall surveys were conducted by electrofishing at five 100-m sites. We refer to all fish detected during the spring (captured in either survey) as “juvenile outmigrants” because we cannot be certain which fish are truly smolts. We anesthetized

all captured fish with MS-222 and inserted a PIT tag into the abdomen through a small incision made by a scalpel. Fish between 65 and 100 mm fork length (FL) were tagged with 12-mm PIT tags, and fish > 100 mm FL were tagged with 23-mm PIT tags.

Spawners

California American Water (the dam owner) captured spawners at the ladder trap from January 1 to May 13, 2019. For each spawner, we visually identified sex and tagged them with a 23-mm PIT tag in the dorsal sinus. The fish were then transported around the dam and released into the reservoir near the spillway. We tagged the first spawner on March 15, 2019, and the last on May 8, 2019. We visually monitored the pool below the spillway on a weekly basis to confirm that spawners were entering the trap and were not holding in the below-spillway pool.

All sample collections were conducted under a California Department of Fish and Wildlife Scientific Collection Permit (S-201120001-20147-002) and an NOAA Section 10(a)(1)(A) Permit (17219-3R) for listed species. Fish handling followed protocols approved by the Institutional Animal Care and Use Committee of the University of California Santa Cruz (Kierj1904).

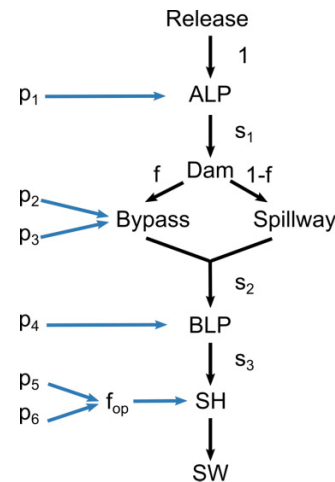
Antenna locations

We used a series of PIT tag antennas to observe fish movements (Fig. 1). The farthest upstream antenna (ALP) was located 0.2 rkm upstream from the head of the reservoir and 0.1 rkm downstream of the RST. We placed one antenna inside the bypass FWC entrance (FWCE) and another on the end of the bypass outflow pipe (FWCP). The paired antennas on the bypass allowed us to observe if fish entered the FWC entrance but did not continue downstream through the bypass pipe. The next antenna was 0.6 rkm downstream of the Los Padres spillway (BLP). Three additional antennas were located in the lower river; two antennas were located at Sleepy Hollow (SH) at rkm 28 and one antenna at Scarlett Well (SW) at rkm 15. We did not have antennas on the spillway, so we inferred spillway passage if a fish was detected downstream of the spillway but was not detected at the FWCE or FWCP antennas.

Transit time and migration speeds

We estimated the transit time between antenna sites (ALP-FWCE, ALP-BLP, FWCP-BLP, BLP-SH, SH-SW), as well as the time from RST-ALP for juvenile outmigrants, and reservoir release-ALP for spawners. Transit time was calculated as the difference between the last detection at the upstream antenna (or release) and the first detection on the downstream antenna. We also estimated the total time spawners spent upstream of ALP, which we considered the “spawning duration”. We inferred the direction of movement at ALP based on detection patterns (Supplement B). We compared migration speeds in the reservoir and river by dividing the distance traveled by transit time. The distance from ALP to BLP was 2.2 rkm, from

Fig. 2. Schematic of the state-space model used to analyze the tagging data. p_i are detection probabilities for each antenna; s_j are movement rates for fish moving downstream between antenna sites. Additional estimated parameters are f , the fraction of fish that used the bypass upon reaching the dam, and f_{op} , the fraction of fish that moved past the SH site when it was operational (accounting for non-operation of this site when both antennas were offline simultaneously). Separate f and s_j were estimated for outmigrants and adults, and separate p_i were estimated for fish with large (23 mm) and small tags (12 mm). The bypass and SH have two detection probabilities (p_i) because there were two antennas at each of those locations.



BLP to SH was 12.4 rkm, from SH to SW was 14.0 rkm, and the spawner reservoir release site-ALP was 1.6 rkm.

Movement rates and detection probabilities

We used a Bayesian mark–release–recapture model to estimate downstream movement rates between antenna sites and antenna detection probabilities (Fig. 2). Movement rates are the proportion of fish that did not disappear between antenna sites. Disappearance may have been due to mortality or cessation of downstream movement.

The model used a discrete state-space formulation, consisting of an observation model for the antenna detection probabilities and a process model for the movement rates, in which observations y_l made at location l are modeled as solely conditional on a hidden state vector z_l , which in turn is modeled as conditional on state in the previous location z_{l-1} . The former conditional probability $Pr[y_l|z_l]$ is the observation model and captures assumptions about the sampling procedure, and the latter conditional probability $Pr[z_l|z_{l-1}]$ is the process model and captures how the state changes over time. Here, because the model addresses downstream movement over time, location and time are treated as interchangeable. Each individual entry $z_{i,t}$ in the state vector represents the state of an individual tagged fish i at time t and can take one of two values: $z_{i,t} = 1$ for a moving fish, and $z_{i,t} = 0$ for a fish that has stopped moving (because of mortality or decision).

For each moving fish, the observation model is a binomial sampling distribution with $N = 1$ and $p_{x,k}$ with the estimated probability of a fish with tag size k being detected at antenna x . For non-moving fish, the probability of detection was set to zero. The multiple antennas at the bypass (FWCE and FWCP) and SH (SH1 and SH2) are treated as secondary sampling occasions within a primary sampling occasion, as in the robust design mark-recapture framework (Pollock 1982; Fig. 2). The robust design assumes that fish passing by the first antenna must also pass by the second antenna (i.e., the movement rate between antennas equals 1). The fraction of fish using the spillway is treated as a component of the observation model for the bypass, estimating the fraction of "excess" fish ($1 - f_j$) for each life-stage j (Fig. 2).

To meet the robust-design assumption at the bypass antennas, we excluded seven fish that entered the bypass (were detected at FWCE), but were not detected in the bypass pipe (FWCP) or at any of the below-dam antennas (BLP, SH, SW), indicating they entered the bypass but did not use it to pass downstream. Of the seven exclusions, three were kelts that were detected at ALP after they were detected at FWCE, thus confirming they did not use the bypass for passage at that time. The remaining four exclusions were juvenile outmigrants, and only one was subsequently detected at ALP after it was detected at FWCE. Excluding these seven fish slightly underestimates the movement rates from ALP to the dam and potentially underestimates downstream passage through the bypass or over the spillway, but we expect this effect to be modest because our tests of the FWCE and FWCP antennas indicated they had very low rates of detection failure.

The process models consisted of additional binomial sampling distributions with parameters $s_{t,j}$, where t specifies the antenna interval (Fig. 2) and j is the life stage. We used neutral priors described by Kerman (2011) and estimated with Markov chain Monte Carlo using four chains with 10 000 iterations each. The last 5000 iterations of each chain were thinned by half, combined, and summarized as posterior probability distributions for the parameters of the model. The model was implemented in Stan (Stan Development Team 2021; Gelman et al. 2013) with the likelihood coded using the forward algorithm to improve computational efficiency (Kery and Schaub 2011; McClintock et al. 2020; Barraquand and Nielsen 2021). We verified chain convergence using the Gelman–Rubin R statistic (Gelman et al. 2013).

Passage flow thresholds

To estimate the lowest spillway depths at which we observed fish passage (i.e., the threshold passage depth), we used reservoir surface elevation data collected by the Monterey Peninsula Water Management District from 2002 to 2021. Reservoir surface elevation was measured at the Los Padres dam spillway crest (the ogee crest) at 15-min intervals using a pressure transducer. Under current conditions, water starts to flow over the spillway crest when the reservoir reaches 317.000 m (National Geodetic Vertical Datum 1929) elevation. We converted reservoir elevation

to spillway-crest-water depth by subtracting 317.000 m from the reservoir elevation. We took the mean daily water depth at the spillway crest on the day a fish was detected at the BLP or bypass antennas to be the passage flow experienced by the fish. We identified the lowest mean-daily spillway-crest-water depth at which juvenile outmigrants and kelts passed over the spillway or through the bypass in 2019.

After we identified the water-depth thresholds, we used them to estimate how often steelhead passage may have been hindered in past years. We calculated the number of days per migration season in which spillway-crest-water depths were greater than the outmigrant and spawner spillway-crest-water depth thresholds from 2002 to 2021. We also estimated the annual severity of passage limitation from 2002 to 2021. We classified years as "moderately passage limited" when 10% of the migration season did not have sufficient spillway depths for passage, and "severely passage limited" when 50% of the migration season did not have sufficient spillway depths for passage. The juvenile outmigrant migration season was based on the 2019 timing in this study. The kelt migration season was based on median historic spawner arrival data at the Los Padres Dam from 1995 to 2018 (Monterey Peninsula Water Management District, unpublished data). We added spawning time and reservoir transit time to the kelt migration season estimates based on observations from this study, and we calculated severity of passage limitation for male and female kelts separately.

Results

We captured 397 juvenile outmigrant steelhead in the RST and tagged 257 with 12-mm PIT tags and 88 with 23-mm PIT tags. We tagged 167 juvenile steelhead during the fall surveys: 86 with 12-mm PIT tags and 81 with 23-mm PIT tags. Of the 126 spawners captured at the Los Padres adult trap, we tagged 84 with 23-mm PIT tags. Antenna detection probabilities, and sample sizes, were high at all antennas for both tag sizes (Supplement C).

Juvenile outmigrant migration speed

Of the outmigrants released at RST and subsequently detected at ALP ($n = 256$), 86% were detected within 24 h of release. The distribution of time between tagging at the RST and detection at ALP was skewed to the left. The median transit time was 9.4 h (inner-quartile range (IQR) 6.8–11.2 h). Juvenile outmigrants that passed downstream over the spillway took approximately 1.5 days longer to arrive at BLP than the juvenile outmigrants that used the bypass. For fish traveling downstream via the bypass, the median transit time from ALP to BLP via the bypass was 31.7 h (IQR 26.2–217 h, $n = 9$). In contrast, fish traveling over the spillway spent a median of 62 h (IQR 27.8–182.0 h, $n = 20$) traveling from ALP to BLP. Very few juvenile outmigrants were detected at BLP–SH and SH–SW antennas, so the transit time estimates should be applied with caution. Median transit time from BLP–SH was 39.1 h (IQR 24.7–447.0, $n = 6$). Only three juvenile outmigrants were detected at both SH–SW, and their transit times were 11.8, 48.9, and 275.0 h.

Table 1. Movement rates and 95% credible intervals between pairs of antennas, estimated from the mark-recapture model.

River segments	Model parameter	Outmigrants	Kelts
ALP-dam	s_1	20% (15%–28%)	87% (69%–100%)
Dam-bypass	f	36% (22%–53%)	2% (0%–7%)
Dam-spillway	$(1 - f)$	64% (47%–78%)	98% (91%–100%)
Bypass/spillway-BLP	s_2	88% (62%–100%)	89% (70%–100%)
BLP-SH	s_3	49% (32%–69%)	91% (79%–100%)

Juvenile outmigrants moved faster in the river than they did in the reservoir; however, the differences were not statistically significant, likely because of small sample sizes. The median in-river migration speed from BLP to SH was $0.32 \text{ rkm}\cdot\text{h}^{-1}$ (IQR $0.03\text{--}0.5 \text{ rkm}\cdot\text{h}^{-1}$). The median reservoir migration speed for juvenile outmigrants passing over the spillway was $0.04 \text{ rkm}\cdot\text{h}^{-1}$ (IQR $0.01\text{--}0.08$; Wilcoxon rank-sum test comparison to in-river speeds: $W = 37$, $p = 0.18$), median reservoir migration speed for juvenile outmigrants passing via the bypass was $0.07 \text{ rkm}\cdot\text{h}^{-1}$ (IQR $0.01\text{--}0.08$; Wilcoxon rank-sum test comparison to in-river speeds: $W = 16$, $p = 0.22$). We did not estimate the migration speed for SH-SW because only three fish were detected at both antennas.

Spawner and kelt migration speed

Most spawners spent less than a day moving upstream through the reservoir, and the median transit time was not statistically different between females and males (Wilcoxon rank-sum test, $W = 482$, $p = 0.43$). The median transit time for females from release to detection at the ALP antenna was 10 h (IQR $4.1\text{--}12.2 \text{ h}$, $n = 39$). The median transit time for males from release to detection at the ALP antenna was 9 h (IQR $5.7\text{--}10.3 \text{ h}$, $n = 22$). Males spent much longer on the spawning grounds than females (Wilcoxon rank-sum test, $W = 88$, $p = 0.004$). Females spent a median of 382 h (IQR $212\text{--}590 \text{ h}$, $n = 33$) on the spawning grounds, whereas males spent a median of 844 h (IQR $643\text{--}991 \text{ h}$, $n = 12$). Once kelts re-entered the reservoir after spawning, they spent 4–6 days before being detected below the dam. The transit times were not statistically different for male and female kelts (Wilcoxon rank-sum test, $W = 147$, $p = 0.98$). Female kelt median reservoir transit time (ALP-BLP) was 100 h (IQR $44\text{--}230 \text{ h}$, $n = 33$) and male kelt median reservoir transit time was 145 h (IQR $48\text{--}178 \text{ h}$, $n = 9$). Transit time from BLP to SH for males and females combined was 16.3 h (IQR $7.05\text{--}19.9 \text{ h}$, $n = 41$). Transit time from SH to SW for males and females combined was 27.4 h (IQR $12.4\text{--}69.7 \text{ h}$, $n = 29$).

After accounting for the distances traveled, kelts moved much faster in the river than they did in the reservoir. The median migration speed from BLP to SH was $0.76 \text{ rkm}\cdot\text{h}^{-1}$ (IQR $0.62\text{--}1.76 \text{ rkm}\cdot\text{h}^{-1}$) and from SH to SW was $0.51 \text{ rkm}\cdot\text{h}^{-1}$ (IQR $0.20\text{--}1.13 \text{ rkm}\cdot\text{h}^{-1}$), whereas the median migration speed upstream through the reservoir was $0.16 \text{ rkm}\cdot\text{h}^{-1}$ (IQR $0.13\text{--}0.28 \text{ rkm}\cdot\text{h}^{-1}$) and downstream through the reservoir was $0.02 \text{ rkm}\cdot\text{h}^{-1}$ (IQR $0.01\text{--}0.05 \text{ rkm}\cdot\text{h}^{-1}$). Both the median migration speeds upstream through the reservoir (Wilcoxon rank-sum tests, $W = 1169$, $p < 0.001$; $W = 1626$, $p < 0.001$),

and downstream through the reservoir (Wilcoxon rank-sum tests, $W = 1572$, $p < 0.001$; $W = 1855$, $p < 0.001$) were slower than both the in-river speeds.

Juvenile outmigrant movements

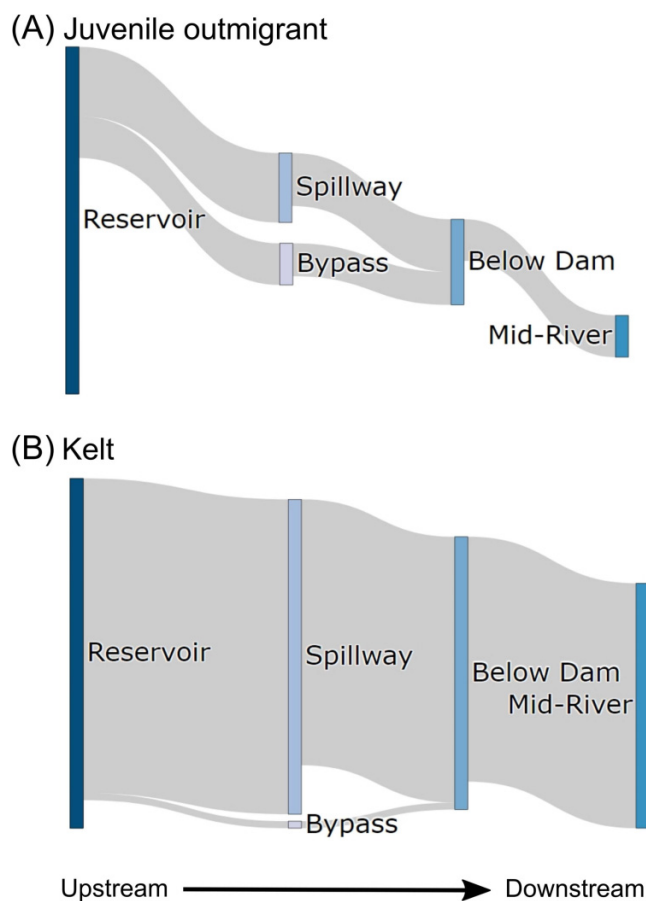
Most of the juvenile outmigrants tagged at the RST were detected at the ALP antenna, which we interpreted as movement into the reservoir ($n = 256/345$). We assumed that the tagged fish that did not enter the reservoir were interrupted by our handling or were not actually migrating when captured at the RST; they are not considered any further in this study. The mark-recapture model estimated that only 20% (95% credible interval (CI) 15%–28%) of the outmigrants that entered the reservoir made it to the dam (Table 1). Of those continuing past the dam, 36% (95% CI 22%–53%) used the bypass to pass downstream and 64% (95% CI 47%–78%) used the spillway. A high percentage (88%; 95% CI 62%–100%) of the juvenile outmigrants that passed over the dam continued 0.6 rkm downstream to the BLP antenna. We were not able to estimate separate movement rates in the lower river (BLP-SH) for juvenile outmigrants that passed via the spillway and bypass because of the low sample sizes relative to the number of model parameters. Only 49% (95% CI 32%–69%) of the juvenile outmigrants that passed the BLP antenna continued downstream to the SH antenna at rkm 28.

The cumulative movement rate, or the product of movement rates, indicates that the majority of juvenile outmigrants did not make it to the mid-river during our study period. Only 9% (95% CI 0%–31%) of the outmigrants that entered the Los Padres reservoir made it to the SH antenna (Fig. 3). The greatest loss, from mortality or outmigration cessation, did not occur after dam passage or in the lower river but instead occurred in the reservoir (Fig. 3; Table 1).

Spawner movements

All but one of the spawners ($n = 83/84$) were detected at the ALP antenna at least once, indicating that very few, if any, spawners stopped or died on their upstream passage through the reservoir. Most spawners (87%; 95% CI 69%–100%) were also able to pass back through the reservoir and downstream of the dam after spawning (i.e., as kelts; Table 1). Of the 14 spawners that did not move downstream of the dam, eight (five males, three females) were not detected after their inbound detection at ALP, suggesting they died on the spawning grounds. The remaining six (four males, two females) spawners that did not move downstream of the dam returned to the reservoir late in the season and were repeatedly detected

Fig. 3. Cumulative movement fractions of juvenile outmigrants (A) and kelts (B) moving through the Los Padres reservoir and Carmel River. The size of the blue lines is the fraction that reached that location, starting with 100% that entered the reservoir. The size of the grey bands is the fraction that moved between locations. [Colour online.]



on the ALP antenna through July 2019, suggesting they were trapped in the reservoir because flows were too low to pass over the spillway.

Almost all (98%, 95% CI 91%–100%) of the kelts that moved downstream of the dam passed over the spillway, while only 2% (95% CI 0%–7%) used the bypass. Three kelts entered the bypass but were subsequently detected at ALP, indicating they entered the bypass but did not use it for passage. These three kelts were excluded from the bypass movement rate estimates. Eighty-nine percent (95% CI 70%–100%) of the kelts that passed over the dam (either via spillway or bypass) continued to the BLP antenna, and 91% (95% CI 79%–100%) moved from BLP to SH. We were not able to estimate separate movement rates in the lower river (BLP–SH) for kelts that passed via the spillway and bypass because of the low sample sizes relative to the number of model parameters.

The cumulative movement rate indicates that the majority of kelts made it to the lower river. 70% (95% CI 62%–85%) of the spawners transported over Los Padres Dam returned to the lower river (SH antenna) as kelts (Fig. 3). The greatest losses

occurred in the reservoir and below the dam (Table 1). Approximately half of the loss in the reservoir can be attributed to post-spawn mortality (based on the number we did not detect moving back into the reservoir), and the other half attributed to impassable flows on the spillway.

Passage depth thresholds

The lowest spillway-crest water depths in which juvenile outmigrants passed over the spillway was 4.9 cm ($1.16 \text{ m}^3 \cdot \text{s}^{-1}$). The lowest spillway-crest water depth in which a kelt passed over the spillway was 8.5 cm ($2.01 \text{ m}^3 \cdot \text{s}^{-1}$). We expected that fish may increase their usage of the bypass once spillway-crest water depths hindered passage; however, that was not the case. The bypass did not assist downstream movement when the spillway was not conducive to downstream passage. The lowest spillway-crest water depth in which a juvenile outmigrant passed through the bypass was 7.3 cm and for kelts it was 9.5 cm.

We interpret 4.9 and 8.5 cm as the spillway passage depth thresholds for juvenile outmigrants and kelts, respectively, for two reasons. First, there were 205 tagged juvenile outmigrants and six tagged kelts above the dam that did not pass once flows declined below the 4.9 and 8.5 cm thresholds. Antenna detections of both life stages above the reservoir (at ALP) indicate that some of those individuals were still alive and could have passed. Second, the reservoir continued to spill over the spillway through July 30 (Fig. 4), when the last kelt was detected at ALP and juvenile outmigrants were still being detected at ALP. In other words, fish were available to use the spillway for passage at water depths less than 4.9 or 8.5 cm, but apparently chose not to do so.

Using 4.9 cm as the juvenile-outmigrant spillway-passage threshold, there were 181 days in 2019 during which juvenile outmigrants could pass over the spillway (Fig. 5). Using 8.5 cm as the kelt spillway passage threshold, there were 150 days in 2019 during which kelts could pass over the spillway. The number of days during which outmigrating juveniles and kelts could pass over the spillway in 2019 was higher than in most years (Fig. 5). For juvenile outmigrant passage, 2019 was tied for the third highest number of passage days since 2002. For kelt passage, 2019 had the most passage days since 2002.

The juvenile outmigration timing in 2019 was such that 50% of the juvenile outmigration occurred by April 30, 2019 and 90% occurred by May 16, 2019. Reservoir transit time was approximately 2.5 days (see section Juvenile outmigrant migration speed), so we estimated that 50% of the juvenile outmigrant passage over the Los Padres dam occurred by May 3 and 90% occurred by May 19. Spawner migration timing estimated from 1995 to 2018 data was such that 50% of the spawners arrived by March 21 and 90% arrived by April 20 from 1995 to 2018 (Monterey Peninsula Water Management District, unpublished data). Spawning and reservoir transit time was 16 days for females and 35 days for males, so we estimated that 50% of the kelt passage over the Los Padres dam occurred by April 6 for females and April 26 for males, and the 90% of the kelt passage over the Los Padres dam occurred by May 6 for females and May 26 for males.

Fig. 4. The frequency of flows in which juvenile outmigrants (A) and kelts (B) passed over the spillway relative to the frequency of all flows over the spillway from March 1 to July 30, 2019. Frequency was smoothed and standardized as a kernel density estimate. The last observed juvenile outmigrant spillway passage occurred at 4.9 cm depth, and the last observed kelt spillway passage occurred at 8.5 cm depth. [Colour online.]

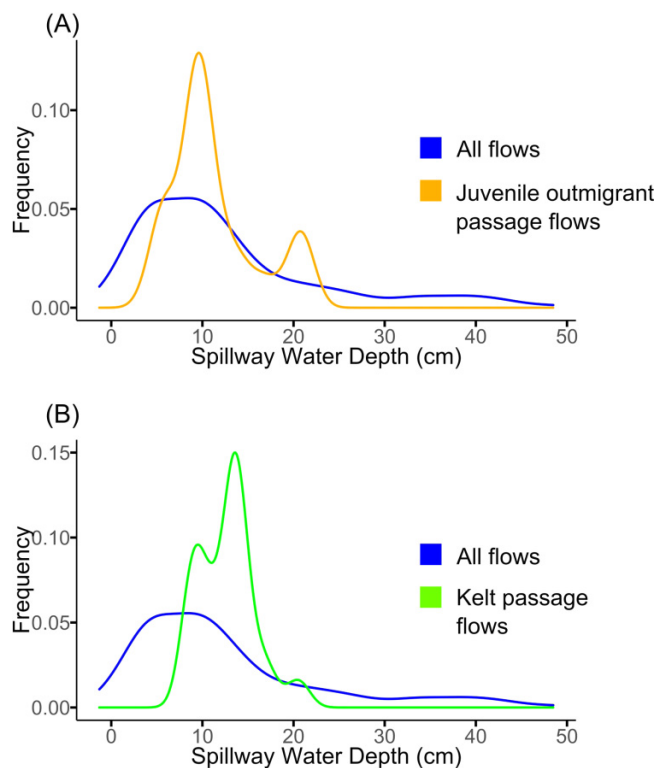
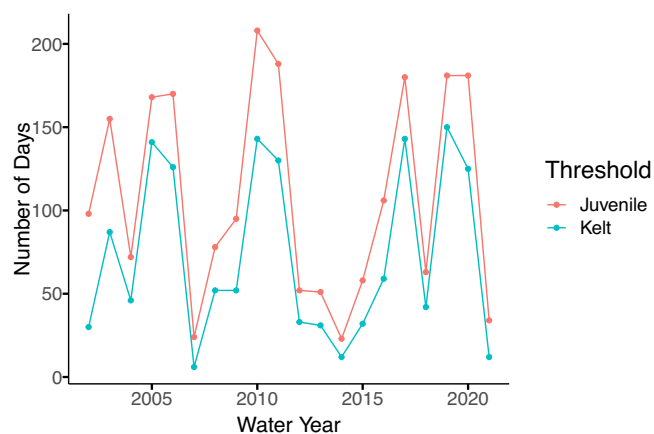
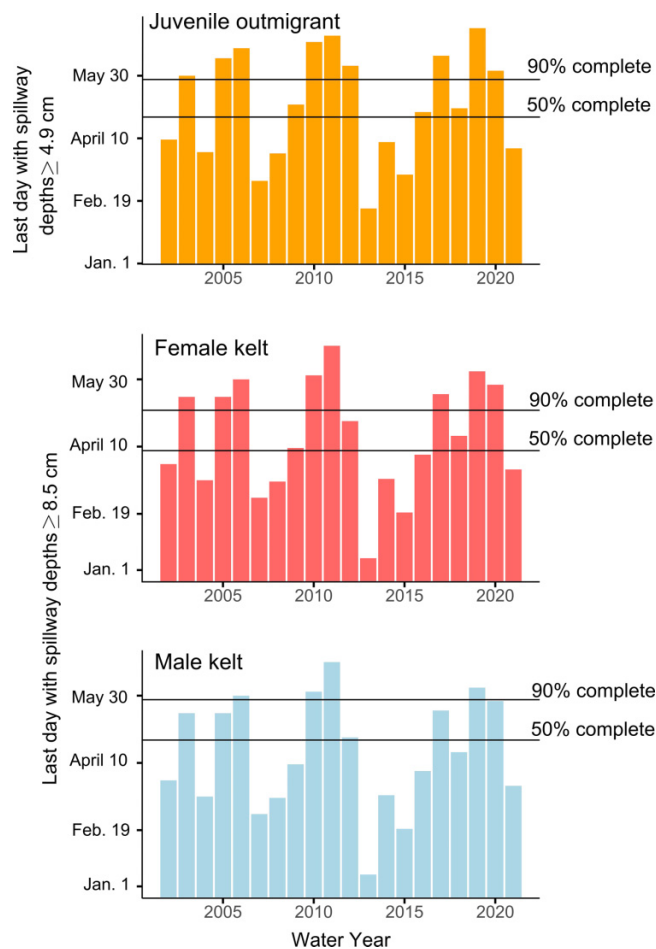


Fig. 5. The number of days in each water year during which water depths exceeded the passage thresholds for juvenile outmigrants (pink) and kelts (blue). [Colour online.]



There were moderate to severe downstream passage limitations for both juvenile outmigrants and kelts in most years from 2002 to 2021. Outmigrant spillway passage was moderately limited in 55% of years, and severely limited in 40% of years (Fig. 6). Female kelt downstream passage was

Fig. 6. The last calendar day of passage flows at the Los Padres spillway varies by year. Years in which flows were below the passage flow threshold before 50% of the outmigration or spawning was complete are considered "severely passage limited", and years in which flows were below the passage flow threshold before 90% of the outmigration or spawning was complete are considered "moderately passage limited". Kelt passage limitations vary by sex because males spend approximately 19 days longer on the spawning grounds than females. [Colour online.]



moderately limited in 60% of years and severely limited in 45% of years (Fig. 6). Male kelt downstream passage was moderately limited in 80% of years, and severely limited in 55% of years (Fig. 6). Male kelts have greater downstream passage limitations because they spend approximately 19 days longer on the spawning grounds than females.

Discussion

The Los Padres fishway provided upstream passage for spawning steelhead in 2019 and, while outmigration was not prevented outright, there is evidence that outmigration was hindered for both juvenile outmigrants and kelts. We observed considerable reservoir loss of juvenile outmigrants, as well as migration delay for both juvenile outmigrants and kelts. Both life stages preferentially used the spillway for

downstream passage, but downstream passage was limited by water depths on the spillway. Fish did not use the downstream bypass when the spillway was too shallow, so it did not appear to expand the temporal window for outmigration. Since there were many periods in which juvenile outmigrant and kelt threshold water depths were not met over the past 20 years, we conclude that the Los Padres Dam has likely limited downstream passage repeatedly over this timeframe.

Adult steelhead have successfully used the fishway to spawn above the dam since 1949 (Monterey Peninsula Water Management District, unpublished data), and a consistent fraction of the spawners that passed a mid-river dam from 1988 to 2015 passed over the Los Padres fishway, indicating that spawners consistently and regularly use the fishway for upstream passage (Arriaza et al. 2017). We were not able to compare the survival of above-dam outmigrants to below-dam outmigrants (juveniles and kelts). However, we assume that survival would be lower for above-dam outmigrants because they face the same migration challenges as below-dam outmigrants once they pass the dam, in addition to the migration challenges caused by the dam and reservoir. Taken together, our results show that the Los Padres fishway cues steelhead spawners to move upstream, but the dam and reservoir present a significant barrier to downstream migration for their offspring and kelts, leading to an ecological trap (Hale and Swearer 2016; Pelicice and Agostinho 2008).

The four factors that limited downstream passage at the Los Padres Dam (water depths on the spillway, loss in the reservoir, migration delay, and avoidance of the bypass) are present at many other dams equipped with fishways, suggesting that ecological traps caused by fishways could be a widespread problem. Ours is the first study to report water depth thresholds for spillway passage of juvenile outmigrant or adult salmonids, even though spillways are the most commonly used downstream passage route at other dams. When spillway passage is possible, fish are much more likely to use spillways for downstream passage compared to alternative routes such as bypasses (e.g., FWCs), turbines, ladders, or sluiceways (Nyqvist et al. 2017a; Skalski et al. 2021). For example, at three Columbia River dams, 80.9% of the radio-tagged steelhead kelts passed via spillway ($n = 504$), compared with 7.5% via turbine ($n = 47$), 6.9% via bypass ($n = 43$), and 4.7% via sluiceway ($n = 29$) in a single year (Wertheimer and Evans 2005). Similarly for juvenile steelhead and Chinook salmon, a meta-analysis of 40 acoustic tag studies conducted from 2010 to 2018 found that spillways were the predominant passage route at Columbia and Snake River dams (Skalski et al. 2021). Additional studies on spillway-passage water-depth thresholds would be useful for quantifying passage limitations, and potential ecological traps, at a broader scale.

We focused on spillway water depths as the main factor limiting spillway passage, but there may be additional compounding factors, such as water temperature. Fish may be prevented from discovering downstream passage routes (i.e., the spillway or bypass) if they are avoiding warm water at the reservoir surface (Caudill et al. 2013). Temperature avoidance may have contributed to the lack of passage for juvenile outmigrants, but probably not for kelts, at the Los Padres

Reservoir in 2019. The last day we observed kelts and juvenile outmigrants passing over the spillway in 2019 was May 23 and June 21, respectively. Water temperatures in the upper 1 m near the reservoir outlet were 16.9 °C on May 10, 18.9 °C on June 7, and 20.2 °C on July 2 (Monterey Peninsula Water Management District, unpublished data). At more northern locations, steelhead start using refuges and avoiding extended exposure around 19–22 °C (Richter and Kolmes 2005; Keefer et al. 2009). Elevated water temperature could be one reason why we did not observe fish using the FWC after the spillway stopped flowing and should be considered when proposing future improvements at the FWC. More broadly, reservoir temperatures could be an additional mechanism by which reservoirs limit downstream passage and create ecological traps, even when downstream passage infrastructure has been provided.

Combined reservoir and dam passage rates (i.e., “reservoir loss”) varied by life stage in our study. Only 20% of the juvenile outmigrants that entered the reservoir continued downstream of the dam, and the probability of moving past the reservoir was lower than anywhere else on their journey. In contrast, nearly all of the in-bound spawners and out-bound kelts passed through the reservoir. Mixed results of reservoir loss have been reported elsewhere (e.g., Kennedy et al. 2018; Babin et al. 2020; Honkanen et al. 2021). For example, juvenile steelhead passing through Snake River dams and reservoirs had combined reservoir and dam passage survival rates ranging from 12% to 100% across 6 years (Muir et al. 2001), whereas juvenile steelhead passing a small inflatable dam in California had a combined average reservoir and dam passage survival of 40% to 63% across 3 years (Manning et al. 2005).

The greater reservoir loss observed in juvenile outmigrants compared to adults/kelts was likely due to several factors. Juvenile outmigrants are more susceptible to predation in the reservoir than spawners or kelts because of their size, and they are more likely to use the reservoir for rearing habitat. Brown trout (*Salmo trutta*) are present in the Los Padres Reservoir and are known to consume juvenile steelhead/rainbow trout in other reservoirs (Wurtsbaugh 1987). There are also several observations to support the hypothesis that juvenile steelhead and rainbow trout (the freshwater resident form) reside in the reservoir after the migration season is over and possibly year-round. A previous study at the Los Padres Reservoir captured more smolts downstream of the dam than entered the reservoir, suggesting that some juveniles remained and smolted in the reservoir from the prior year (Chaney 2015). Additionally, anglers catch (355–550 mm) rainbow trout (resident steelhead) and smaller juveniles (<150–200 mm) in the reservoir from September to October (California Department of Fish and Wildlife, unpublished data). These observations indicate that some of the juvenile outmigrants we lost in the reservoir could have ceased downstream movement for the purpose of rearing and smolted the following year. We could not assess the percentage of rearing juveniles because our study was conducted for a single season only. If a high percentage of the lost juvenile outmigrants smolted the following year, then the reservoir loss aspect of the ecological trap would be less than we estimated over

a single study year. The fate of juvenile outmigrants in the reservoir, and therefore the degree to which the Los Padres Reservoir itself contributes to the ecological trap, is a worthwhile topic for future research.

Migration delay in reservoirs has been observed elsewhere, including for steelhead kelts (Keefer et al. 2004; Wertheimer and Evans 2005), juvenile steelhead (Raymond 1968, 1979), and other juvenile salmonids (Carr 1999; Babin et al. 2020). In our study, juveniles migrated through the reservoir 4–8 times more slowly than they migrated downstream through the river, and outbound kelts migrated downstream through the reservoir 30–45 times more slowly than they migrated downstream through the river. The reduced water currents and increased swimming effort in the reservoir may have contributed to this slowing (Mesa and Magie 2006); however, results from recent studies on Atlantic salmon (*Salmo salar*) smolts using high-resolution tracking methods indicate that the migration delay was probably caused by many back-and-forth movements in an apparent attempt to find the reservoir outlet (Honkanen et al. 2018; Babin et al. 2020). Notably, back-and-forth movements and the additional time spent searching for the outlet are not unique to reservoirs but have also been observed in natural lake systems (Honkanen et al. 2021). Migration delay through a reservoir does not directly limit downstream passage, but it could indirectly limit downstream passage if passage routes are seasonally blocked, as they are at the Los Padres Dam. Migration delay could also be especially costly for juveniles that are susceptible to predation (Nygqvist et al. 2017b; Kennedy et al. 2018). Thus, although migration delay does not directly limit downstream passage, it could nonetheless contribute to formation of an ecological trap through increased energy expenditure and predation, especially in places where the number of passage days depends on rainfall or other varying conditions.

The bypass was moderately effective at providing downstream passage for juvenile outmigrants but ineffective at providing downstream passage for kelts. An estimated 36% of juvenile outmigrants passed downstream via the bypass, while only an estimated 2% of kelts used the bypass. We are not aware of studies that have examined kelt collection efficiency at other bypasses; however, there is comparable data on juvenile outmigrant collection. Juvenile steelhead collection efficiency data were collected at four FWC bypasses in Washington and Oregon at large reservoirs (2837–932 019 ML; Kock et al. 2019). The collection rates for fish released at the head of reservoirs were bimodal with two FWCs having very high collection rates (90% and 94%) and two FWCs having very low collection rates (11% and 19%). That the Los Padres FWC bypass collection rate sits between these values suggests that it is not the most effective but is also not the least effective. Kock et al. (2019) found that inflow volumes and guidance nets were positive predictors of FWC collection efficiency (across Chinook (*Oncorhynchus tshawytscha*), coho (*Oncorhynchus kisutch*), sockeye (*Oncorhynchus nerka*), and steelhead), but that effect of FWC entrance size was greatest when the forebay area was large. The Kock et al. (2019) result suggests that increases in inflow volumes and the addition of netting at the Los Padres FWC bypass could improve the juvenile collection success at the Los Padres Dam bypass.

Given the problems with downstream passage identified in our study and elsewhere (Pelicice et al. 2015), it seems reasonable to ask at what point are we doing more harm than good by allowing fish to pass upstream via fishways? In other words, when should managers prevent fish from using fishways to pass upstream until better downstream passage can be achieved? Quantifying how much population recruitment is lost to lack of downstream passage is a key component of this management decision, but it is not the only factor that should be considered (Pompeu et al. 2012; Birnie-Gauvin et al. 2019). Not all losses to recruitment will result in population declines, and some decrease in recruitment may be a worthwhile trade-off if there are other benefits of upstream passage. For example, in large watersheds such as the Columbia River, some populations are endemic to locations upstream of the dams and there is limited spawning habitat below the dams (Skalski et al. 2021). In cases such as these, some losses to recruitment may be a worthwhile trade-off of limited downstream passage. A population life-cycle model, or similar model, could be used to determine whether losses due to downstream passage justify preventing fish from moving upstream via fishways.

Providing downstream passage at dams is a formidable challenge because it requires not only passage at the dam itself but also through the reservoir. Compared to the science and technology of upstream passage, downstream passage is a relatively young field and there is still much to be learned. Better solutions for downstream passage for a wide array of species are needed (Pelicice and Agostinho 2008). As dams continue to be built and operated worldwide (Zarfl et al. 2015; Flecker et al. 2022), and fish populations continue to decline (Hall et al. 2012), solutions for downstream passage cannot come soon enough.

Acknowledgements

Thomas Christensen, Beverley Cheney, and Kevan Urquhart (MPWMD) contributed valuable knowledge and loaned us the RST. Fieldwork assistance was provided by Brennan Helwig, Jordan Besson, Tim Paulson, Issac Rodriguez, Dan Atkins, and Eric Lumas. Gus Wathen and Vince Tranquilli contributed to the antennas. Mike Garello provided dam and FWC specs. Aman Gonzalez, Chris Rudolph, Robert Coppola, and Tony Lapham at Cal-Am Water provided logistical support. Funding for the project was provided by Cal-Am Water (SWFSC Agreement No SWC-156) and the NOAA Cooperative Institute for Marine, Earth, and Atmospheric Systems (CIMEAS). Joel Casagrande, Nate Mantua, Dave Rundio, Alyssa Fitzgerald, Fernando Pelicice, and two anonymous reviewers provided feedback on an earlier version of this manuscript.

Article information

History dates

Received: 12 May 2022

Accepted: 19 July 2022

Accepted manuscript online: 5 August 2022

Version of record online: 20 October 2022

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Data availability

Data and code are provided in Dryad at <https://doi.org/10.7291/D1T97T>.

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All authors contributed to the development of this manuscript. HAO: conceptualization, data curation, formal analysis, investigation, methodology, project administration, supervision, visualization, writing-original draft. DNC: investigation, writing — review and editing. GB: methodology, writing — review and editing. CH: investigation, resources, writing — review and editing. EPP: project administration, writing — review and editing. DAB: conceptualization, formal analysis, funding acquisition, project administration, writing — review and editing.

Competing interests

The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2022-0095>.

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