

Carmel River Fisheries Report 2021

Revised Final: June 18, 2021

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In fulfillment of the Memorandum of Agreement SWC-156



NOAA FISHERIES | Southwest Fisheries Science Center
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION



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1 Revision Description

The previous final version of this report, dated May 28, 2021, was revised to add steelhead rescue data from the Carmel River Steelhead Association in years 1997-2013 that was previously omitted in the Fish Rescue Chapter (Chapter 4). The description of mitigation and restoration actions in the Introduction was also expanded to more accurately reflect the history of mitigation and restoration in the Carmel River.

2 Introduction

The purpose of this report is to describe the status of the Carmel River steelhead population and the results of on-going research within the watershed. Carmel River steelhead returns have declined significantly from historic numbers, and unfortunately have continued to decline on the shorter timeframe for which we have data. After low returns in the early 1990's, returns increased for about 10 years before beginning a more steady decline through the present (Figure 1). The decline is even more stark when considering a rough index of population growth (e.g., the number of returns per parent from 3-4 years prior; Figure 1), which shows a more consistent decline than the returns themselves.

These continued population declines are concerning, but are also disheartening given the considerable investments in both mitigation and restoration. Some of the main restoration actions have included the following. California American Water and the Monterey Peninsula Water Management District (MPWMD) successfully restored the riparian vegetation in the lower mainstem following its near-total loss in the early 1990's. They added 2,500 tons of spawning gravel to replace gravels entrained behind the Los Padres and San Clemente dams (MPWMD 2020). California American Water decreased aquifer pumping from an average of 16,700 acre feet annually in the early 1990's to an average of 7,500 acre feet in the five year period from 2015-2020, and they restricted their summer pumping at upper valley wells to increase summer stream flows in the upper valley. The south arm of the lagoon was restored and habitat improvements, such as root wads, were installed by the Carmel River Steelhead Association (CRSA). The San Clemente Dam was removed in 2016 to improve fish passage and sediment transport. Smaller fish passage barriers, such as culverts and seasonal dams, have been removed by CRSA, Trout Unlimited, and other local partners.

In addition to this restoration, there have been extensive mitigation actions. Fish 'rescues' were initiated by CRSA in the mid-1980's to save juvenile

steelhead and rainbow trout from drying stream sections. These efforts have expanded to include MPWMD's fish rescue program, which began in 1989, and now includes the Sleepy Hollow Rearing Facility, which began operating in 1996. Additional assisted-rearing actions have included a juvenile-to-smolt steelhead rearing program in 1981-1986, and a captive broodstock program from 1990-1994, both of which were conducted by CRSA. The upstream ladder at the Los Padres dam was improved in 1999, through combined efforts of California American Water, CRSA, MPWMD, California Department of Fish and Wildlife (CDFW), and the National Fish and Wildlife Foundation. In 2017, California American Water installed a downstream fish bypass at the Los Padres dam with the intention of improving habitat connectivity within the watershed. Water conservation outreach has decreased water use per household (i.e., per connection) from approximately 0.5 acre-feet per household annually to approximately 0.23 since 2014 (MPWMD 2020).

Yet, despite the considerable mitigation and restoration efforts, the steelhead returns have not rebounded. Part of the reason may simply be the delay between actions and population-level responses, which are expected to take several, if not more than, 3-4 year generations (i.e., 16-20 years). It is also likely that water use and habitat loss within the watershed continue to impair the population. For example, nearly 50% of the watershed goes dry during the summer due, in part, to human water use (Figure 8). The lower river and lagoon are disconnected during the critical summer months in almost every year (Figures 3, 8), the lagoon is regularly breached during winter to prevent flooding, which results in unstable and lost lagoon fish habitat, and downstream fish passage at the Los Padres dam continues to be a problem (Boughton et al. 2020).

Teasing apart these various possible causes of the persistently low steelhead returns requires the ability to a.) separate the influence of freshwater conditions from marine conditions on the productivity shown in Figure 1, and b.) determine how the steelhead population responds to particular mitigation of restoration actions. The longstanding monitoring scheme to count the number of spawners at Los Padres Dam, and measure juvenile densities in the fall, gets us some portion toward this goal, but not completely. In 2017, we implemented a PIT tagging program to address the two key data gaps. The use of PIT tags allows us to track individuals and examine the effects of specific mitigation actions, such as fish rescues. It also allows us to estimate smolting rates (% juveniles emigrating to the ocean in spring per year), which we identified as a key piece of information for disentangling the relative influences of freshwater and marine conditions. For example, if juvenile densities are high but smolting rates are low, we can identify and remedy the causes of

low smolting rates. Similarly, if smolting rates are high but marine survival is low, we can consider actions on the freshwater side that are known to improve subsequent marine survival.

In this report we describe preliminary results of our PIT tagging studies, and two additional analyses that were done with MPWMD long-term monitoring data. We examine how summer flow conditions influence juvenile steelhead density (Chapter 3), and we describe the history of fish rescue efforts within the watershed (Chapter 4). We estimate smolting rates for 2017-2020 using PIT tags (Chapter 5). Note that we do not report smolting rates for the current year (2021), because the smolt migration was still underway at the time of report publication. We also use the PIT tag data to characterize movement patterns within the watershed and compare patterns of fish tagged during fall population surveys with fish tagged as relocated rescues and summer lagoon-rearing juveniles (Chapter 6). We identify the tagged juveniles that have returned to spawn (Chapter 7), we assess the length characteristics of tagged emigrants and spawners (Chapter 8). We then compare trends in adult returns of Carmel River steelhead to other California populations and identify shared regional population drivers (Chapter 9). Finally, we summarize this information into an overall statement on the status of Carmel River steelhead and provide adaptive management recommendations (Chapters 10 and 11).

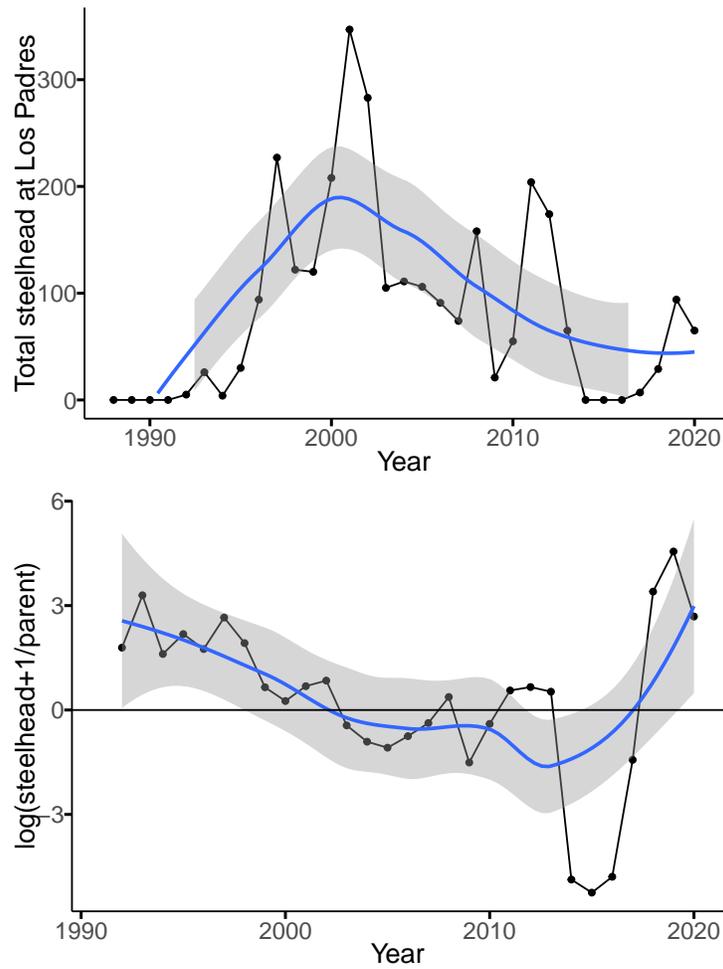


Figure 1: The number of adult steelhead spawners captured at the Los Padres dam in the Carmel River (a) and the number of steelhead spawners at Los Padres converted to productivity (b). Productivity is the number of anadromous spawners at Los Padres (log transformed and added to 1) divided by the number of anadromous parents from 3-4 years prior (Equation 4). The overall population decline is more obvious after transforming to productivity.

3 Assessment of streamflow and juvenile production in the regulated portion of the Carmel River

The flow of the Carmel River between Los Padres Reservoir and the Pacific Ocean is regulated by a variety of anthropogenic mechanisms—releases from Los Padres Reservoir, fundamentally, but also by pumping of groundwater from the aquifers underneath Carmel Valley. California American Water and numerous other smaller water users have well sites distributed throughout the valley whose use has the capability to lower the water table locally and dewater the channel (Kondolf 1982). In 1993, California American Water agreed to manage its wells to withdraw water from valley aquifers as far west (as far downstream) as practical during the summer low-flow season, in order to minimize effects on surface flow of the river. Here we take a look at the effects of this strategy on production of juvenile steelhead in the regulated portion of the Carmel River.

We expect to see that surface flow is more consistent, and steelhead production has improved, in the eastern part of Carmel Valley as a result of this strategy. Unfortunately we have no substantial record of the production of juvenile steelhead prior to 1993 to estimate production before the change in operations. Since 1993 however the Monterey Peninsula Water Management District has consistently collected data on juvenile steelhead production each fall in the eastern Carmel Valley, and also in the western Carmel Valley (which still gets dewatered) and in the canyon section of the river upstream of Carmel Valley. The canyon has only a small aquifer with minimal groundwater pumping and so flows there are dominated by dam releases. We can therefore compare these three areas (Canyon, Upper Valley, Lower Valley) to get a good sense of how the management of the groundwater withdrawals in the Valley has affected steelhead production (Table 1).

Table 1: Hypotheses of steelhead production based on Carmel River aquifer conditions.

Domain	Aquifer	Groundwater Withdrawal	Water Table	Steelhead Production
Canyon:	Small	Small	High	Baseline (Control)
Upper Valley:	Large	Small	High	?
Lower Valley:	Large	Substantial	Low or variable	Low?

Methods

Process Domains We treated the three domains (Canyon, Upper Valley, and Lower Valley) as distinct process domains. Process domains are spatially identifiable areas characterized by distinct suites of geomorphic processes that control the geomorphology and hydraulics of the channel (Montgomery 1999). For our analysis here, the Canyon domain is defined as the river channel between Los Padres Dam and the confluence of Tularcitos Creek near the head of Carmel Valley. The Upper Valley is the river channel between Tularcitos Creek and the Narrows midway down the valley, and the Lower Valley is the river channel from the Narrows to the estuary just west of Highway 1.

The Canyon domain is characterized by a highly confined channel in a V-shaped canyon where channel position is controlled by the canyon slopes. The channel runs through the accumulated alluvium at the base of the V, which typically only supports a small aquifer immediately under the channel and adjacent terraces. Sediment dynamics are dominated by hillslope inputs and transport of sediment from upstream sources through the domain to downstream sinks (Montgomery and Buffington 1997). Flow regime in the summer is dominated by releases from Los Padres Dam.

The Upper and Lower Valley domains are characterized by a channel meandering through a deep and wide alluvial valley with a large underlying aquifer. Streambanks and position of the channel are controlled by deposition of sediment and woody vegetation stabilizing the banks, which in turn is dependent on the underlying aquifer, and the position of the channel can change drastically in response to effects of droughts and floods on streamside vegetation and geomorphic units (Harrison et al. 2017; Kondolf 1982). Sediment dynamics are dominated by deposition of sediments from upstream sources (Montgomery and Buffington 1997). Flow patterns in the summer arise from an interaction of upstream dam releases, evaporation, and infiltration into the underlying aquifer. When the water table is low the dam releases tend to completely infiltrate leaving a dry channel; if the water table falls too low for too long, riparian trees can also die, destabilizing the banks and the channel (Kondolf 1982).

The Upper and Lower Valley domains have similar natural processes as described above, but strikingly different anthropogenic processes. These two domains are separated at the Narrows by an underground bedrock sill that effectively separates them into two distinct aquifers. Historically both aquifers were tapped as a water supply by California American Water, but this exacerbated the natural tendency of the channel to dry out during the summer low-flow season due to infiltration. In 1993 the water company agreed to

minimize the effects of its water withdrawals on aquatic flora and fauna by pumping from the aquifer as far downstream as possible each summer, so that the Upper Valley domain and portions of the Lower Valley domain would retain continuous surface flow for as much of the summer as practical. Since that time, the channel has tended to lose surface flow in some or all of the Lower Valley each summer, but maintain it in the Upper Valley. Here we ask whether this has been an effective strategy by testing if fish production in the Upper Valley has been higher than in the Lower Valley, and comparable to the Canyon domain.

Stock-recruit function To estimate the relative fish production of the three process domains, we used nonlinear regression to fit a stock-recruit model. Stock-recruit models estimate the production of ‘recruits’—in this case young-of-the-year (YOY) juvenile steelhead that survive to the end of the dry season—as a function of number of adult spawning fish and various environmental factors. For environmental factors, here we consider a fixed effect of each process domain, various aspects of flow conditions in the river channel, and background variation from other unspecified factors.

Specifically, the regression model had number of spawners N_t as a predictor for juvenile production $J_{D,t}$ in each domain D in each year t , but augmented with parameters for a fixed effect of spatial domain (β_D), the effect of low-flow condition $Q_{D,t}$ in each domain, and the effect of releases of relocated juveniles $T_{D,t}$ in each domain,

$$J_{D,t} = s_1(N_t) + s_2(Q_{D,T}) + \beta_d + \alpha T_{D,t} + \epsilon_t + \epsilon_x \quad (1)$$

Here, $J_{D,t}$ is the number of juvenile *O. mykiss* produced at the end of the dry season (Sep – Oct) in each domain in each year. The two functions $s_1(\dots)$ and $s_2(\dots)$ each represent a smooth curve describing the effect of spawner abundance and flow condition on fish production, respectively. To avoid making any prior assumptions about the form of these curves, we parameterized them as thin-plate regression splines (Wood 2006). Thin-plate regression splines allow an estimated curve to be as wiggly as is optimal for out-of-sample prediction (i.e. generalization to other years not in the data set), and thus allow us to identify the shape of the predictable effects of spawner abundance and flow as suggested by the data themselves.

The β_D term represents three parameters ($D \in \{1, 2, 3\}$) describing the fixed effect of each process domain on production, while α represents the proportion of relocated fish released in each domain in each year ($T_{D,t}$) that survive to the end of the dry season.

The final two terms in the model are residual error ϵ_x and a random effect of year ϵ_t , each assumed to be normally distributed. The random effect for year represents year-to-year background variation in the production of juvenile steelhead, as distinct from the effects of spawner abundance, flow conditions and relocations. This estimated year effect competes with the two curves s_1 and s_2 to explain variance, and thus serves as an implicit null model: if the variation in juvenile production from year to year is simply due to random fluctuations unrelated to spawner abundance or flow, this random effect will explain all or most of the variance, telling us that spawner abundance and flow conditions do not predict production.

Number of spawners For N_t we used the annual count of adult steelhead ascending San Clemente Dam. This count is incomplete because it omits steelhead that spawned in habitat downstream of the dam site, which includes about half of the Canyon domain and all of the Upper and Lower Valley domains. Numbers of steelhead spawning in these portions of the stream network are not known. We assume these numbers to be directly proportional to the number spawning upstream of the dam site (and thus counted at the ladder).

This assumption is supported by data from redd surveys (surveys of spawning nests) that have been conducted sporadically in the system since the late 1990s. On six occasions redd surveys were conducted extensively both downstream and upstream of the dam site within two weeks of each other, allowing us to examine whether redd densities were proportional below and above the dam site. The six points lie roughly along a straight line passing through 0,0 (Figure 2), supporting the assumption of proportionality. Fortunately, these six surveys captured most of the range of spawner (and redd) densities observed over the past 30 years, from a low of around 1 observed redd per kilometer to a high of 6 observed redds per kilometer of stream habitat, so we have confidence that the assumption is reasonable over the full range of spawner abundances observed in the counts.

A notable feature of Figure 2 is that, while the redd densities below and above the dam are proportional, they are not the same—redd densities tend to be lower downstream of the San Clemente Dam site, suggesting that some portions of the downstream habitat are not used by steelhead for spawning. The counts N_t at San Clemente Dam ceased after 2015 with removal of the dam. Before this time they were highly correlated with the counts made upstream at the Los Padres Dam fish trap, so we used linear regression to predict post-2015 counts at the former dam site using the Los Padres counts

as predictors.

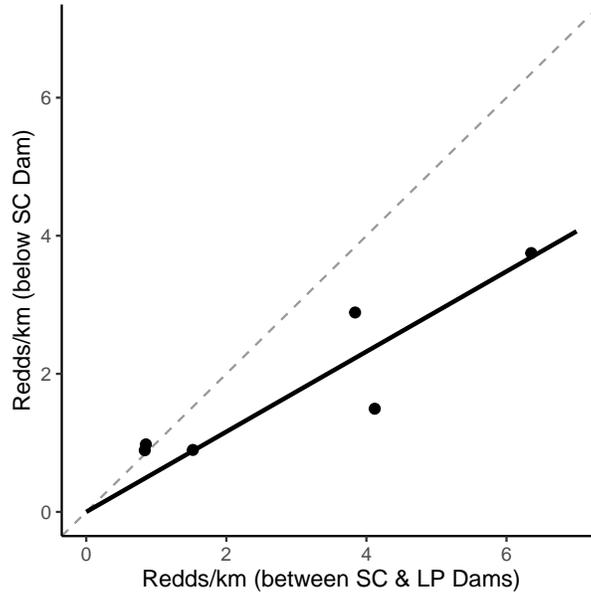


Figure 2: Observed redd densities above and below the San Clemente Dam site on six occasions when redds were extensively surveyed both above and below the Dam site.

Flow condition We compiled various flow statistics for $Q_{D,t}$ and compared their ability to predict juvenile production to get a sense of how flow condition affects production. Statistics were compiled from four gauges operated on the regulated portion of the river since at least 1993 (Table 2). The SH, DJ, and NC gauges represent flow conditions local to each process domain, so local flow statistics were compiled for each record of juvenile production $J_{D,t}$ by using the gauge within the corresponding domain D. We also considered predictors from just the RR gauge, representing the overall river flow prior to any infiltration into either aquifer, and predictors from just the NC gauge, representing river flow near the western end of the Lower Valley where effects of infiltration are likely the highest.

We used flow statistics to entertain two general hypotheses: that production is controlled by conditions during the low-flow season (July – September), by limiting the amount of habitat available to rearing juveniles; and that production is controlled by conditions during the end of the wet season (March – May). High flows during this spring period may limit production by scouring

Gauge Code	Name	Location
SH	Sleepy Hollow	within Canyon domain
RR	Robles del Rio	Upper Valley near Canyon transition
DJ	Don Juan Bridge	within Upper Valley domain
NC	Near Carmel	within Lower Valley domain

Table 2: Stream gauges used in the analysis.

redds or flushing YOY out to sea. Low spring flows may trap smolts prior to emigration and thus inflate the production data estimated the following fall. For both the spring and summer periods we considered as predictors the annual values for mean local flow, median local flow, the 10th percentile of local flow and the 90th percentile. We also considered the predictive value of these statistics for the RR gauge, representing flow prior to infiltration, and the NC gauge, representing after infiltration and the state of the fish movement corridor to the estuary, which is also used for rearing.

Relocations To obtain numbers of relocated fish released into each domain in each year, we reviewed the annual records of rescue activities conducted each year since 1993. Field notes were used to identify which domains fish were released into, and the annual number for each was summed excluding those *O. mykiss* identified in the notes as resident adults.

Juvenile production The Monterey Peninsula Water Management District has conducted fall population surveys of juvenile steelhead densities at selected sites throughout the three domains since the early 1990s. To estimate juvenile production, we used these data to estimate mean density (fish per unit length of channel) in each process domain, and multiplied it by the wetted length of channel at the end of the dry season in the fall. These estimates include YOY juveniles, older juveniles (1 year or older), and resident adult *O. mykiss*, the non-migratory form of the species. However, in previous reports we described how the vast majority of juveniles captured in fall surveys are YOY, so we used the total fish densities (all age and size classes) to approximate YOY densities.

The densities are generated from depletion-electrofishing, in which a section of stream is temporarily isolated using block nets and repeatedly sampled for fish using an electrical field that temporarily stuns fish, allowing them to be netted. Repeated passes of the electrofisher yield diminishing counts, and the steepness of the decline in counts can be used to estimate the total number of

fish, including those not captured. We obtained the complete record of original depletion counts from MPWMD and estimated densities using the method of Carle and Strub (1978) as implemented in the software package FSA (Ogle et al. 2021).

The length of wetted channel at the end of each dry season was estimated by inferring a dry-map from the field notes on rescues. An initial dry-map was constructed for each year by assuming that sections of streams listed as rescue sites in that year subsequently dried up. This map was then compared to electrofishing data and gauge data and adjusted if either of these sources showed that surface flow was retained at the end of the dry season (i.e. if fish were sometimes rescued from sites that subsequently retained surface flow). These last two steps only led to small adjustments in the inferred dry-map. Last, we compared our inferred dry-maps for 2006 through 2013 to detailed dry maps made by the MPWMD in those years. We found them to closely match, suggesting our approach for inferring dry-maps for the longer timespan 1990 – 2019 was robust.

Statistical analysis Once these various datasets had been assembled, we fit the stock-recruit function to them using non-linear regression. Specifically, we fit various versions of the model using the `mgcv` package of the statistical software system R (Team 2020; Wood 2006), which allowed us to estimate the spline curves s_1 and s_2 simultaneously with the random effect of year. An initial run of model-fitting found that residuals did not meet assumptions of the statistical model (normal distribution, constant variance), and so a square-root transformation was applied to $J_{D,t}$, which addressed the issue.

We compared various versions of the stock-recruit function using AIC, the Akaike Information Criterion (Burnham and Anderson 2002). AIC measures the ability of a model to make good out-of-sample predictions (e.g. predictions in future years). Models with different combinations of predictors can be compared via their AIC score, which thus identifies the model or models with the most useful (predictive) combination of predictors. Typically it is not the AIC score itself that is informative, but the difference in AIC between models. A difference (Δ AIC) of zero or only a few points indicates models that have similar predictive power, whereas differences of 6 or more indicate a substantive difference. These differences can be represented in slightly more intuitive form as evidence ratios, which give the odds that one model versus the other will make better predictions of new data.

We used AIC to compare models in two stages. In the first stage, we fit the base stock-recruit function (the equation above) using each of the various

candidates for flow condition $Q_{D,t}$. In the second stage, we used the top-ranked model from stage 1, and compared it to modified versions in which individual predictors had been removed ($N_t, Q_{t,D}, D$), potential interaction terms were added ($N_t \times D, Q_{D,t} \times D$), or a linear rather than a curved response was assumed ($N_t, Q_{D,t}$).

Results

The inferred dry map (Figure 3) showed that the western part of the Lower Valley consistently dried up in all but five years. Generally most of the Lower Valley dried up. After 1993, groundwater withdrawals began in the western Lower Valley each summer and moved east as needed, and this appears to have protected surface flows in the Upper Valley. However, the Lower Valley is still mostly dewatered in most years. A small section of the Upper Valley dewatered in most years; this is a section of accumulated alluvium in the western part of DeDampierre Park in Carmel Valley Village, likely due more to geomorphic processes accumulating sediment than to water withdrawals. However, the size of this dry zone expanded for two years during the recent drought.

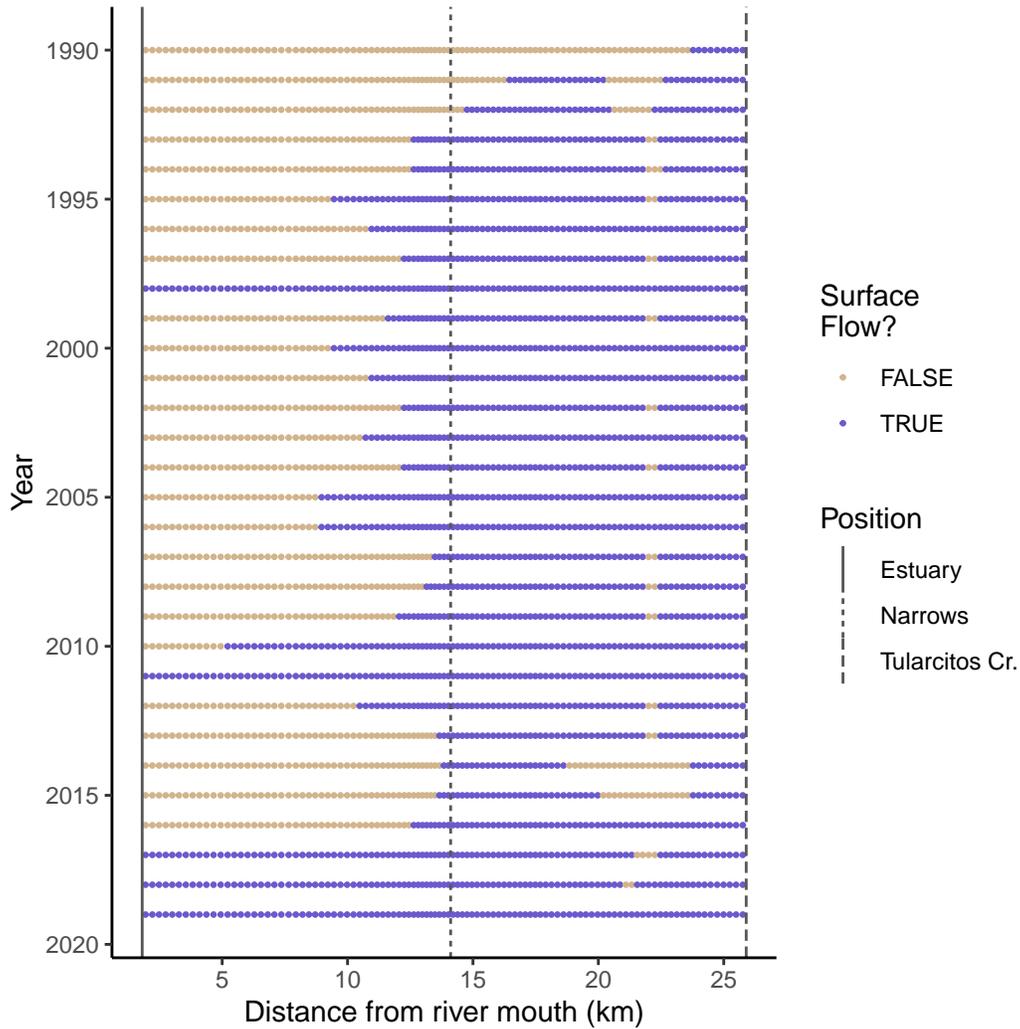


Figure 3: Map of the maximum extent of dry channel each year as inferred from records of fish relocations. Vertical dashed line shows approximate location of the Narrows.

For the first stage of fitting the stock-recruit function, we compared versions with different statistics for flow condition. We found the top-ranked model to have local summer median flow as a predictor, though mean flow performed nearly as well as median flow (Table 3). None of the spring flow metrics, or the metrics based only on one gauge (RR or NC) performed nearly as well as the four metrics for local summer flow. For example, models with some version of spring flow as the predictor were always less than 1/2000th as likely as median

Flow Predictor¹	K	AIC	DAIC	Evidence Ratio²
Local Summer Median	28.5	842.8	0.0	1:1
Local Summer Mean	27.9	844.3	1.4	1:2
Local Summer 10th %	27.8	848.0	5.1	1:13
Local Summer 90th %	26.9	848.6	5.8	1:18
Local Spring 10th %	23.6	858.3	15.5	1:2300
RR Spring 90th %	24.4	858.4	15.6	1:2400
NC Spring 90th %	24.3	858.4	15.6	1:2400
NC Spring Mean	24.1	858.5	15.6	1:2500
RR Spring Mean	24.0	858.5	15.7	1:2600
NC Spring 10th %	23.6	858.9	16.0	1:3000
Local Spring Median	23.9	859.0	16.2	1:3200
RR Spring 10th %	23.0	859.1	16.2	1:3400
Local Spring Mean	24.2	859.6	16.7	1:4300
Local Spring 90th %	24.5	859.9	17.0	1:5000
NC Summer Mean	22.1	860.1	17.2	1:5500
RR Summer Mean	23.6	862.0	19.1	1:14,000

Table 3: Stage-1 model selection for prediction of juvenile production from flow conditions.

¹ Local = NC gauge for the Lower Valley, DJ gauge for the Upper Valley and SH gauge for the Canyon.

² Relative to top-ranked model.

summer flow to give the best predictions (See evidence ratios in Table 3). We conclude that local flow during the low-flow season is the key hydrologic control on juvenile production. Releases of water from Los Padres Dam, as represented by the RR gauge, were not good predictors of juvenile production, because they did not account for subsequent infiltration in the upper and lower Valley. Connectivity to the estuary, as represented by the NC gauge, was also not a good predictor of juvenile production, nor were the local flow conditions during the spring when YOY steelhead are either inside redds or first emerging from the gravel, and smolts of the previous years' cohorts were migrating to the ocean.

The top-ranked model in Table 3 explained 91.7% of the deviance in the juvenile production estimates. Its summary table (Table 1) showed that all the predictors within the stock-recruit function were statistically significant ($p < 0.01$), often highly so ($p < 0.001$). Diagnostic plots of the residuals (see Figure 4) show good behavior, although there are some modest artifacts

A. Parametric terms	Estimate	SE	<i>t</i>	<i>p</i>
Intercept (Canyon)	162.6110	8.9154	18.2394	<0.0001
Domain: Upper Valley	-31.2596	7.4547	-4.1933	0.0001
Domain: Lower Valley	-99.0289	11.8836	-8.3332	<0.0001
Relocations	0.3186	0.1182	2.6949	0.0091

B. Smooth terms	edf	Ref.df	<i>F</i>	<i>p</i>
Spawner Abundance (<i>N</i>)	2.1344	2.3110	13.8995	<0.0001
Summer Median Flow (<i>Q</i>)	2.8573	3.4574	4.8484	0.0056
Random effect of Year	16.2455	27.0000	1.6776	0.0003

Table 4: Terms of the top-ranked model from stage-1 model selection.

of the lower production estimates having a boundary at zero (left sides of the various panels in Figure 4). Despite this, there is good support for the assumptions of normally-distributed residual error (bottom left panel of Figure 4) and constant variance over the range of prediction (top and bottom right panels of Figure 4). We conclude that spawner abundance, median July – Sept flow, number of relocated fish and the characteristics of the process domain all show detectable effects on fish production, even when annual background variation from other limiting factors is also taken into account.

Table 5: Estimates of mean annual production in each process domain.

Process Domain	Regression Terms $\sqrt{\# \text{ fish}}$	Mean Production (# fish)	Total Channel (km)	Fish per km	Relative to Canyon
Canyon	162.6	26,439	15.2	1739	100%
Upper Valley	162.6 - 31.3	17,240	11.8	1463	84%
Lower Valley	162.6 - 99.0	4,045	12.3	329	19%

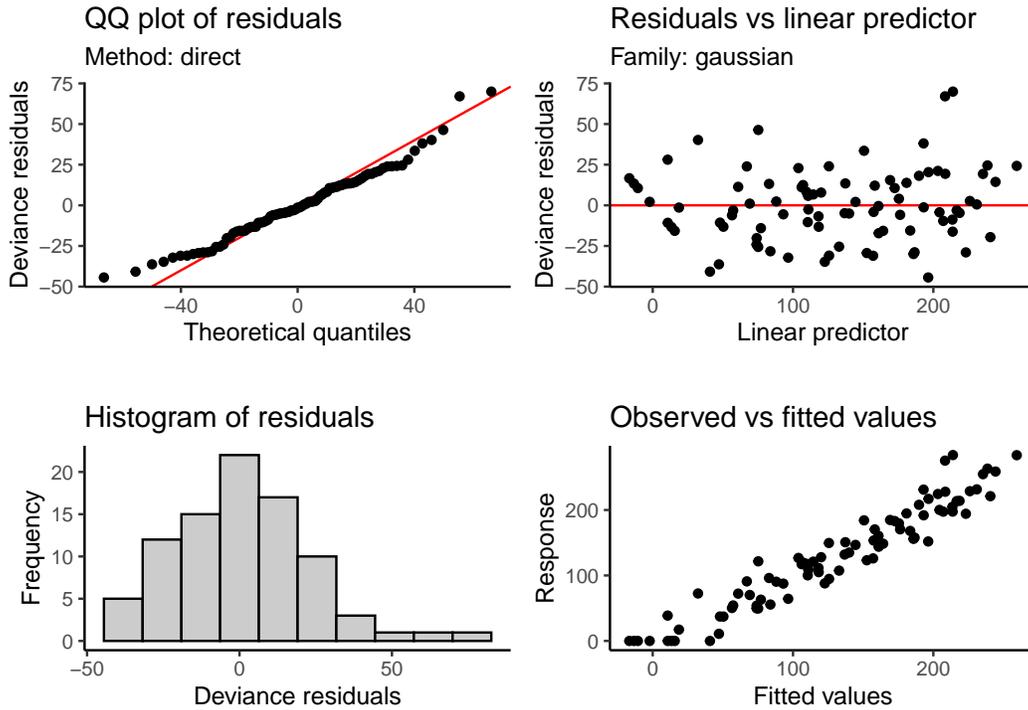


Figure 4: Appraisal of model assumptions for the base model (top-ranked model from stage-1 selection, using local summer median flow to represent Q).

The fixed effects of the process domains (Table 5) are parameterized as an intercept representing mean production in the Canyon, and deviations from the intercept representing production in the Upper and Lower Valleys (negative deviations in both cases). Recalling that the fish production estimates were square-root transformed before fitting the regression, the mean production in the various process domains can be calculated from the regression terms (Table 5). We observed a substantial difference in production per unit kilometer of

stream channel for the Upper and Lower Valleys, with production in the Upper Valley about 4.5 times higher. Neither has as high production as the Canyon per unit of stream channel, but the Upper Valley comes close.

The effect of the relocations on fall production was about 0.32, though this parameter needs some care in interpretation due to the square-root transformation. For consistency we square-root transformed the release numbers as well as the fall production; on a linear scale the effect translates to about 0.10 fall recruit per released fish on average. That is, over the life of the rescue operation, the regression suggests that on average about 1 juvenile was recruited to the fall juvenile cohort for every 10 fish relocated the previous summer or spring. Here we use relocation to refer to fish rescued from a drying section of channel and immediately (same day) released back to the wild in a wet section rather than being taken to the Sleepy Hollow Rearing Facility.

The spline curves estimated for spawner abundance and for local summer flow can be observed in the top two panels of Figure 5. For spawner abundance, the spline curve showed the classic behavior of a stock-recruit curve, with production initially increasing in proportion to spawner abundance, but leveling off at higher numbers of spawners, in this case when $N > 500$. This suggests that the available habitat becomes saturated above 500 spawners, although we should stress that this analysis does not account for fish rearing in the estuary. It could very well be the case that recruits saturate the river habitat at around 500 spawners but that extra fish would move to the estuary so that the true recruitment curve continues to rise past 500 spawners. However, in most years the drying in the lower river would block such movement in the late summer or fall.

The spline curve for local summer flow (Figure 5, top right) shows a surprising hump-shaped effect on fall production. Initially the production increases with flow as would be expected since the amount of habitat in late summer appears to function as a bottleneck on production. However, this positive effect of flow levels off around $0.3 \text{ m}^3/\text{s}$ (or about 10 cfs) and subsequently declines, suggesting that higher summer flows actually have a detrimental effect on instream juvenile production. This is a surprising finding which we revisit below. But first let's look at the second stage of model selection.

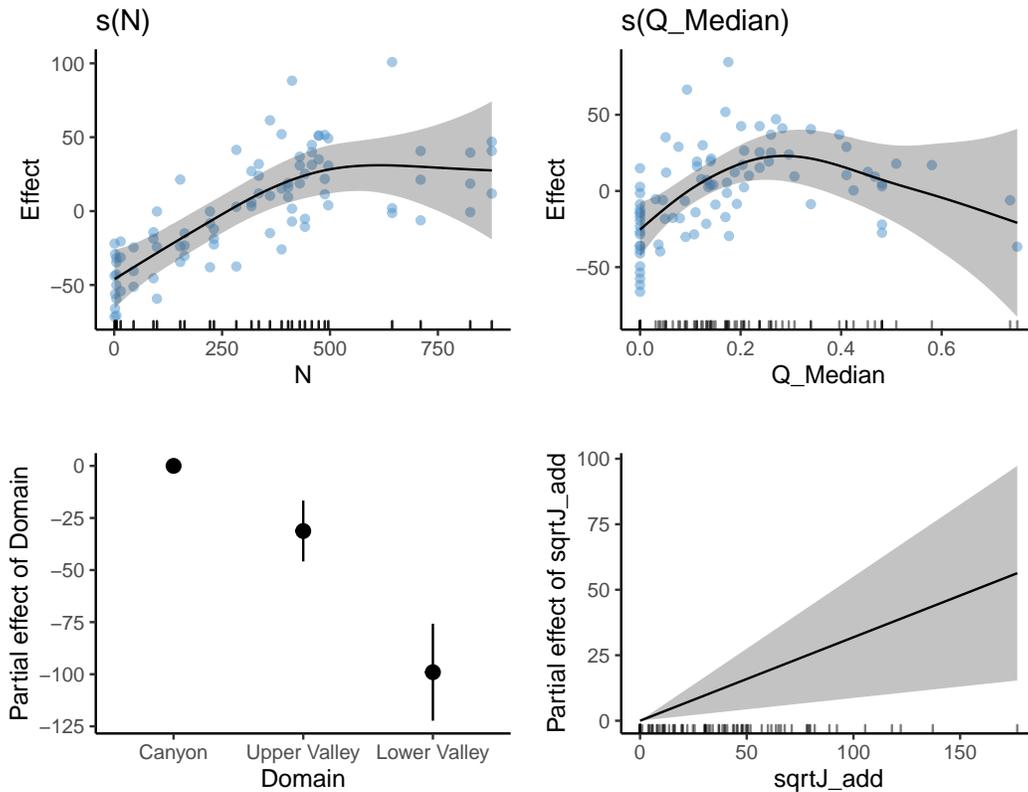


Figure 5: Partial effects of the various predictors in the base model. Vertical axes show square root of juvenile production relative to production in the Canyon in an average year (Effect = 0). The four panels show the effects of spawner abundance (N), local summer flow (Q_{median}), process domain, and relocations ($\sqrt{(J_{\text{added}})}$). Gray bands and vertical bars show 95% confidence intervals for each effect; dots in the top two panels are partial residuals of the data used to fit the curve.

In the second stage of model selection, we took the top-ranked model shown in Figure 5 and compared it to modified versions in which individual predictors had been removed ($N_t, Q_{t,D}, D$), potential interaction terms were added ($N_t \times D, Q_{D,t} \times D$), or a linear rather than a curved response was assumed ($N_t, Q_{D,t}$). Again using AIC to compare the predictive ability of the various models, we find that three and possibly four models rose to the top (Table 6). Our base model ($N + Q + D$) was one of these, at the second rank slightly below a model in which the effect of spawners was assumed to be linear ($LN + Q + D$, no leveling off as was observed in the top left of Figure 5). However, these two

Table 6: Stage-2 model selection for parsimony and interaction effects.

Model	K	AIC	DAIC	Evidence Ratio
LN + Q + D	29.1	841.0	0.0	1:1
N + Q + D	28.5	842.8	1.9	1:2.6
N x D + Q	32.7	843.6	2.7	1:3.8
Q + D	31.5	844.9	3.9	1:7
N + Q x D	31.5	849.3	8.3	1:64
N + D	24.8	857.1	16.2	1:3300
N + LQ + D	24.4	859.5	18.5	1:11,000
N + Q	27.7	889.6	48.7	1:4×10 ¹⁰

LN is linear effect of spawners, *LQ* is linear effect of flow.

models have similar AIC scores and essentially the same predictive power (the top-ranked model is only 2.6 times more likely than the second-ranked to make the best predictions). The third-ranked also has quite similar predictive power to these two; this model included an interaction between spawner abundance and process domain. Finally, a model in which spawner abundance was simply omitted as a predictor also performed fairly well ($Q + D$ in Table 6). The interpretation of this model is not that spawner abundance is unimportant to juvenile production, but that it is always sufficient to saturate habitat so that other limiting factors explain the variation in recruitment.

Recalling for a moment the humped effect of summer flow in the base model (top right panel of Figure 5), we direct attention to the model $N + LQ + D$ in Table 6. This model is identical to the base model except it assumes a linear response of production to flow. We observe in Table 6 that it had very poor predictive ability, with only 1 chance in 11,000 of making better predictions than the top-ranked model. It's evidence ratio with the base model (rank 2) is only 1:4200, also quite poor. Thus we can conclude that juvenile production does not simply increase with more summer flow, and that the interpretation of leveling off above $0.3 \text{ m}^3/\text{s}$ is strongly favored by the data.

We also see that this hump-shaped effect of flow is consistent across the four top-ranked models. In Figure 6 we have plotted the juvenile production that is predicted by each of these four models, under varying spawner abundance (left column) and under varying summer flow (right column). We see that while the models disagree somewhat in the effects of spawner abundance on fish production, they all agree rather well on the effects of summer flow. All show an initial rise to a peak around $0.3 \text{ m}^3/\text{s}$, followed by decline at higher flows, though the steepness of the decline varies somewhat among the models.

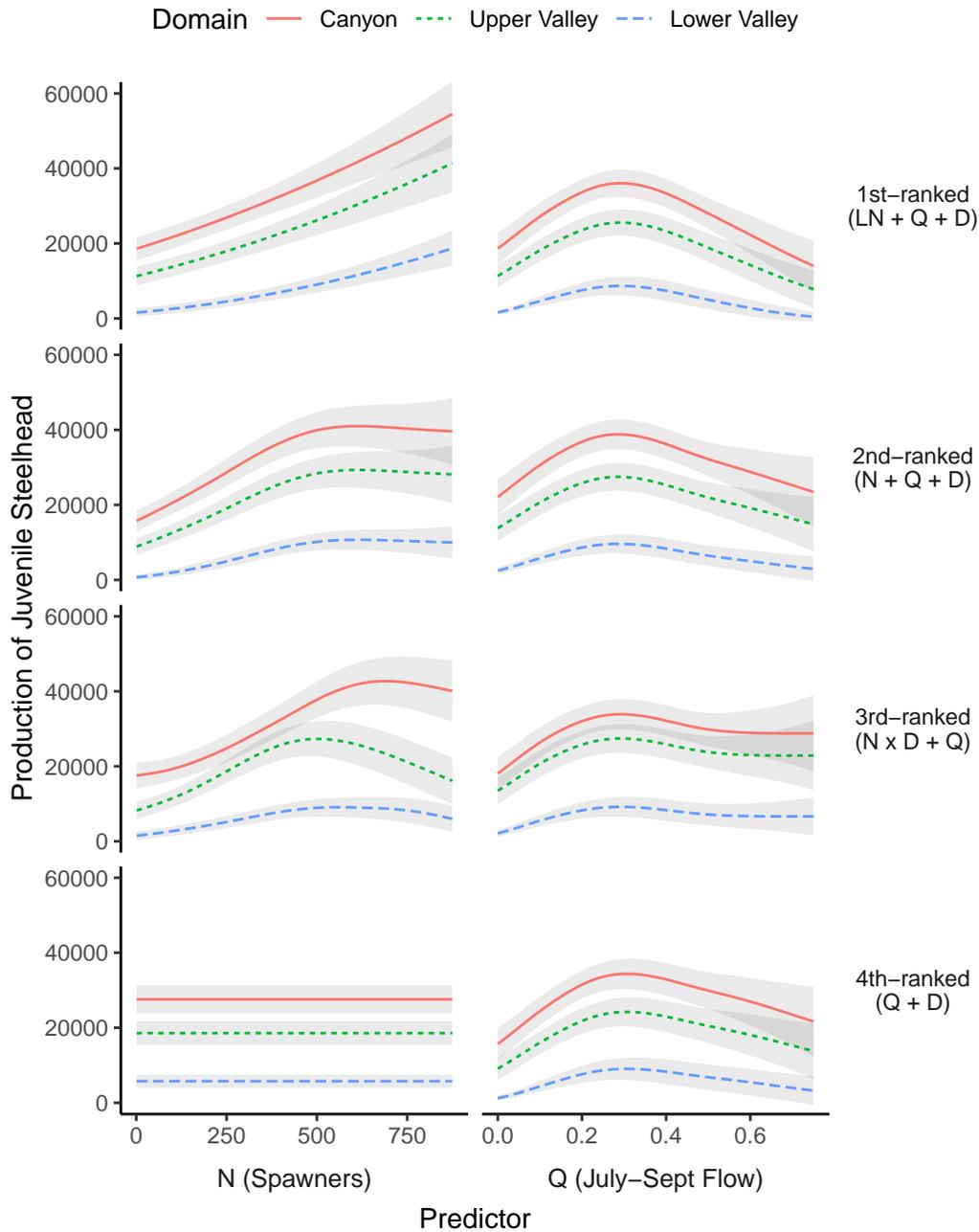


Figure 6: Predictions of the four best models from stage-2 selection, including the base model in rank 2. Predictions of the right column were made for average flow conditions, average year effect, and zero relocations; predictions for the left column were made for average spawner abundance, average year effect and zero relocations.

What could be the explanation for this decline at high summer flows? We cannot resolve this question in the current analysis, but here we discuss some possibilities. First, it seems unlikely that flows greater than $0.3 \text{ m}^3/\text{s}$ are themselves having direct negative impacts on juvenile *O. mykiss*. Elsewhere this species is tolerant of much higher flows and faster water velocities. If high water velocities were a problem, we would expect them to manifest more strongly in the spring when flows were higher on an absolute scale, and more likely to scour redds or flush the newly-emerging young of the year downstream. But we find that spring flow conditions are much poorer predictors of juvenile recruitment than summer flow conditions.

In internal discussions we identified three possible explanations for this decline in apparent production at higher summer flows, two of which might actually represent a benefit to steelhead production. There may be other plausible explanations as well. First, these wetter years may support higher growth rates for juvenile steelhead (Arriaza et al. 2017). This could drive lower densities because larger fish defend larger territories (Dunham and Vinyard 1997; Grant and Kramer 1990; Keeley 2003). The excluded smaller fish would either emigrate, die, or persist somewhat in marginal habitats, although the latter would not lead to the lower observed densities that we observed at higher flows. Higher growth rates exhibited by fewer fish may actually be a benefit because these fish are more likely to survive their entry into the ocean and have higher rates of return as adult steelhead (Arriaza et al. 2017; Bond 2006).

Second, these wetter years are more likely to maintain a connection of surface flow with the estuary throughout the summer, which gives juvenile fish the opportunity to move from the river channel to the estuary and exploit the feeding opportunities there. In California, estuaries of coastal streams typically close off from the ocean seasonally, forming freshwater lagoons during the dry season. These lagoons can provide very rich feeding opportunities for juvenile steelhead, producing large fish that are more likely to survive their entry into the ocean and return as adult steelhead (Bond 2006). Perhaps the lower fish densities observed in the mainstem at flows above $0.3 \text{ m}^3/\text{s}$ reflect not poorer survival at higher flows, but the movement of fish downstream to the estuary prior to the surveys at the end of the dry season. In Scott Creek, juveniles move downstream and into the lagoon in spring, rear there until late summer when water quality deteriorates, and then return upstream in late summer and fall before outmigrating as smolts the following spring (Hayes et al. 2011). However, our tagging data demonstrate that most juveniles migrated back upstream in the early winter in 2019, despite having access to the river in late summer that year (Section 6).

To evaluate the plausibility of fewer fish as a result of lagoon access, we

replotted the partial effect of flow from the base model (Figure 5, top-right panel), but with the residuals color-coded as to whether a continuous connection of surface flow was maintained with the estuary in the year represented by the residual. What we see is that the descending limb of the hump corresponds almost entirely to years in which a connection was maintained with the estuary (Figure 7). The residuals are also coded by process domain, and show that the decline is exhibited by all process domains, not just the Lower Valley immediately adjacent to the estuary. This suggests (though we stress it does not prove) that connection with the estuary is a switch-point representing two different modes of fish production in the Carmel River, and that the hump-shaped effect of flow reflects this switch point.

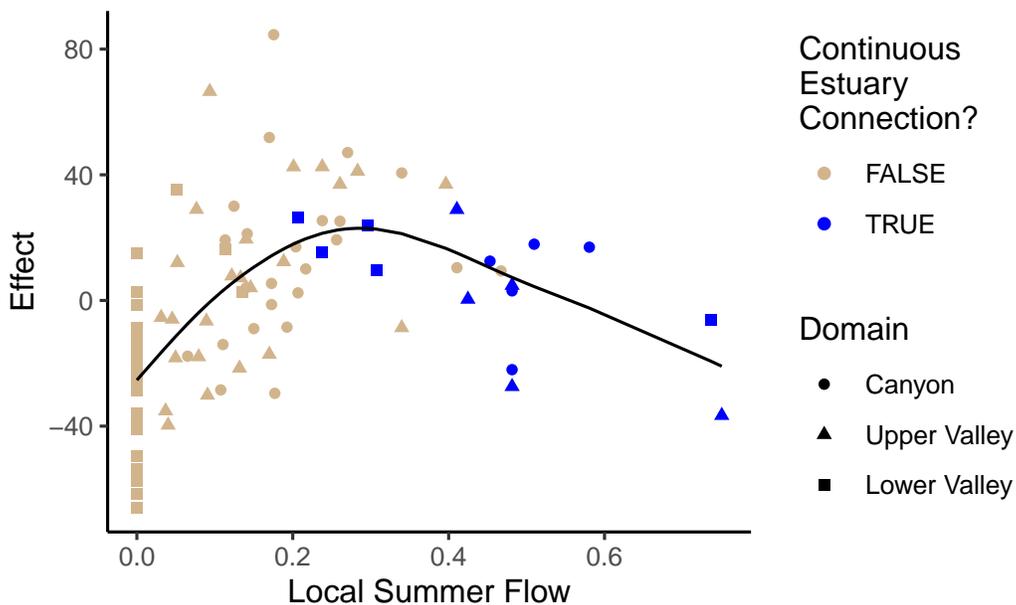


Figure 7: Potential switch-point driving the hump-shaped response. Connection with the estuary was estimated as a daily surface flow of at least $0.03 \text{ m}^3/\text{s}$ ($\sim 1 \text{ cfs}$) being maintained at the NC gauge for the entire low-flow season (July – September)

Cohorts of juvenile salmonids can respond to high densities (crowding) by increased mortality or lower growth rates, but they can also respond by increased emigration, and fish will emigrate—a behavioral response—well before they risk mortality, if conditions allow for it (Einum et al. 2006). The hump itself in Figure 7 could therefore reflect a situation where densities are high

enough to stimulate emigration, but because the estuary is not connected the fish in fact have nowhere to emigrate to. Thus the decline in observed production above $0.3 \text{ m}^3/\text{s}$ could actually represent a benefit for steelhead, if it is an artifact of increased use by the population of the estuary. In this case the switch point suggested by Figure 7 would represent the point at which the cohort's response to crowding shifts from lower growth and higher mortality to emigration downstream to the estuary.

More broadly, what the switch-point represents is an opened connection to a fourth process domain—the dry-season estuary—and this opening can produce a variety of impacts and benefits to steelhead. While the opening may allow juvenile steelhead to exploit feeding opportunities in the estuary and reduce crowding in the river, it would also allow piscivorous fish species in the estuary to move upstream during the summer low-flow season and prey on steelhead. In particular, Striped Bass (*Morone saxatilis*) have been observed using the estuary since at least the 1980s (Dettman and Kelley 1986), and have sometimes been captured in the hundreds in recent years (Boughton 2020). During periods when the river is connected to the estuary, Striped Bass have been observed at various locations in the Canyon, Upper Valley and Lower Valley domains and are probably preying on native stream fishes, including juvenile steelhead, though the extent of the impact is not known. Thus, the apparent decline of steelhead production observed above $0.3 \text{ m}^3/\text{s}$ could also represent a true decline in overall production due to Striped Bass predation.

Our main conclusions in this section are that:

1. The pumping strategy of Cal Am has generally been effective at maintaining surface flow in the Upper Valley, although the recent drought led to some losses.
2. Average fish production in the Upper Valley has been nearly as high (85%) as in the Canyon, in units of fall juveniles per kilometer of river channel.
3. Most of the Lower Valley is still routinely dewatered and fish production suffers accordingly. On average fish production in the Upper Valley is 4.5 times higher than in the Lower Valley.
4. Local summer flow (July – September) had more predictive power for juvenile production than any other flow metric we examined.
5. We found a very robust pattern that fish production improved with summer flow, up to a peak at around $0.3 \text{ m}^3/\text{s}$ (~ 10 cfs), after which it declined.

6. The mechanism for the decline is unclear. It may correspond to increased fish growth or increased movement into the estuary, both of which could reflect lower juvenile production in river but higher overall production of adult steelhead. Conversely, it may represent a true decline in fish production due to predation by Striped Bass.
7. The relationship between juvenile densities and number of returning adult spawners remains unclear because we do not know what proportion of these juveniles survive to the following spring and then emigrate as smolts, and whether this smolting rate has scope for management. This is why we have focused so much energy on PIT tagging and estimating smolting rates (Chapter 5).

4 Fish rescues

Fish rescues are one of the major mitigation efforts undertaken in the watershed and are conducted by MPWMD and CRSA. In a typical year, the Carmel watershed will lose about 50% of its wetted habitat during the summer from a combination of its Mediterranean climate and the associated dry season, aquifer pumping, and surface water use (Figure 3). Habitat loss primarily occurs in the mainstem lower river from Valley Greens Drive to the lagoon and a small section at Carmel Valley Village, as well as in most tributaries (Figures 3, 8). In an effort to save juvenile steelhead and rainbow trout in the drying habitats and maintain the overall steelhead run, MPWMD and CRSA ‘rescue’ fish in the drying areas. Rescued fish are either relocated to wetted habitat (typically upstream) or the Sleepy Hollow Rearing Facility.

To summarize the rescue efforts, we estimated the number of rescue occasions and the number of fish rescued in different river zones based on field notes and data received from MPWMD and CRSA. We expect some modest level of error in our river zone assignments due to the occasional difficulty in identifying the landmarks in the field notes. The river zones include the Lower Valley (Highway 1 to the Narrows), Upper Valley (the Narrows to Tularcitos Creek confluence), Lower Canyon (Tularcitos Creek confluence to old San Clemente Dam site), Upper Canyon (old San Clemente Dam site to Los Padres Dam). Each tributary is also a separate river zone (Cachagua, Garzas, Hitchcock, Potrero, and Robinson Canyon subbasins), as is the lagoon (from the ocean to Highway 1).

Fish rescues have been frequently conducted in the past 31 years. The Lower Valley is the most often rescued river zone and rescues have taken place

there in 30 of the past 31 years (years 1989-2020; Figure 9). The Upper Valley has been rescued in 20 of the past 31 years. The tributary subbasins have also been extensively rescued, including 22 years in Cachagua and Garzas creeks and 20 years Hitchcock and Robinson Canyon creeks. Potrero Creek was rescued less often, in 8 of the past 31 years. The lagoon was also rescued in 8 years. The Lower Canyon and Upper Canyon have been rescued far less often, in 6 and 4 years, respectively.

A total of 678,872 steelhead and rainbow trout have been rescued and relocated since 1989. Of those fish, 228,405 have been reared at the Sleepy Hollow Rearing Facility since 1996. The vast majority of rescued fish have come from the Lower Valley, where 487,922 fish have been rescued (Figure 10). The second highest number of fish rescued is from Cachagua Creek at 99,891 fish. The number of rescues from the remaining river zones ranges from 334-27,162 fish (Figure 10).

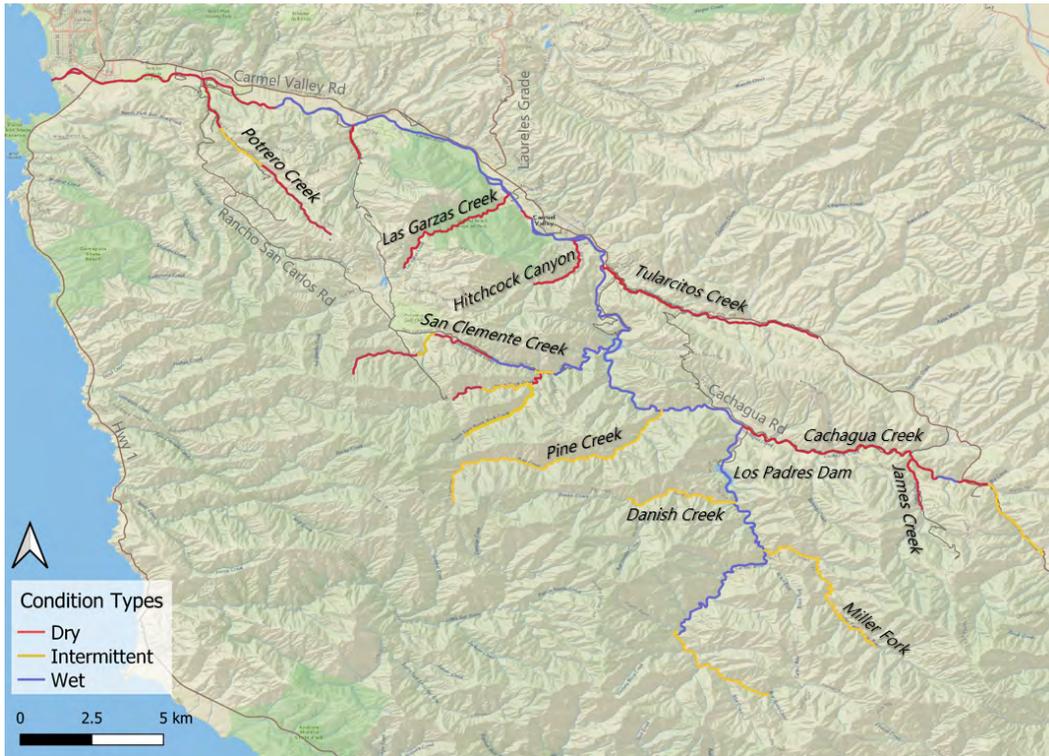


Figure 8: Typical summer (July-October) stream flow conditions in the Carmel River watershed. ‘Wet conditions’ are when water is flowing in both pools and riffles, intermittent conditions are when pools and riffles are disconnected or stream sections that may or may not be wet in an average year. Dry conditions are when there is no water in the channel in an average year. Stream sections were categorized into condition types based on local knowledge of the watershed received from Cory Hamilton (MPWMD), Brian LeNeve (CRSA), and Bruce Dormody. The yearly conditions in all sections upstream of the Los Padres Dam and Pine Creek are not well documented, so those condition designations should be interpreted with caution.

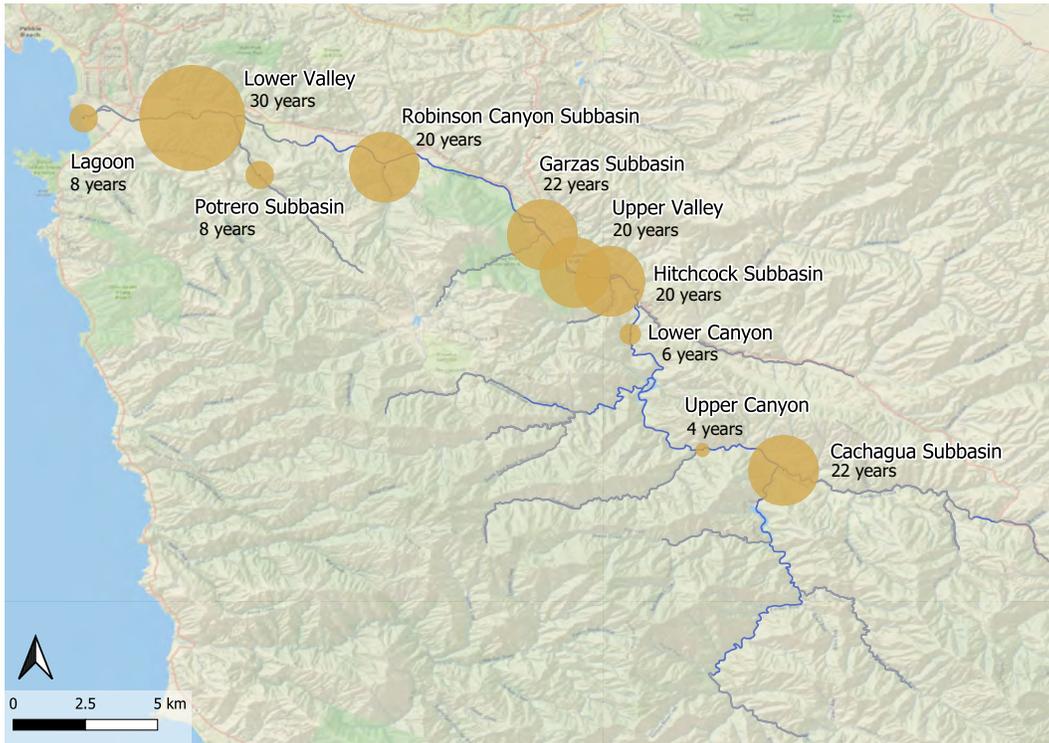


Figure 9: The number of years different river zones have been rescued by MPWMD and CRSA from 1989-2020.

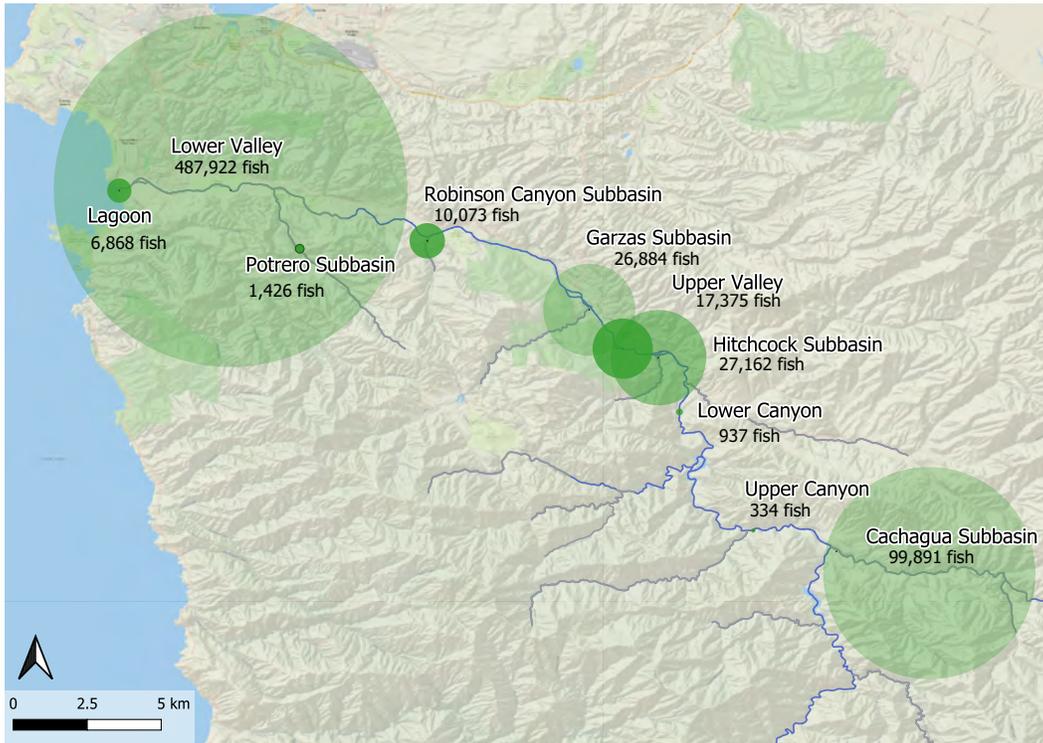


Figure 10: The total number of fish rescued from different river zones from 1989-2020. Rescues were conducted by MPWMD and CRSA.

The extent to which rescue efforts have been successful is largely unstudied, both in the Carmel River and in other populations where rescues occur. Arriaza et al. (2017) modeled fish growth and survival from 1996-2013 and found a correlation between the number of captively reared fish that were released and the subsequent adult returns, suggesting that most of the returning adult steelhead since 2005 had been captively reared at Sleepy Hollow Rearing Facility. At the same time, they found that relocation rescues may have reduced the steelhead runs slightly by raising competition and decreasing growth. However, this was based on inference from modeling and was not conclusive due to the confounding of rescues and low water years (i.e., the slower growth in years with rescues may have been due to smaller river flows).

To assess the effectiveness of rescues more directly, MPWMD began PIT tagging all rescues larger than 65 mm FL starting in 2018. As we discuss in detail in subsequent chapters, our preliminary results show that approximately 8% smolted in 2019 (from the 2018 tag year; Table 7). Additionally, one Sleepy Hollow Rearing Facility captively reared fish returned as a spawner from the

2016 cohort and 6 relocated rescues returned as spawners from the 2018 tagging effort (Table 8). We are planning future analyses to assess the smolt-adult return rate and to compare smolting rate with fall-tagged fish. However, these preliminary data clearly indicate that rescues can result in anadromous returns, in the sense that some rescues smolted and some of those returned to spawn. The more nuanced questions such as whether rescues inadvertently harm local fish at relocation sites or what is the relative effectiveness of relocating versus rearing rescues are questions that we will continue to address with PIT tags.

5 Smolt Production

MPWMD's long-term population monitoring scheme has estimated juvenile abundance at the end of each dry season (i.e., 'fall population surveys'), but does not determine what proportion of these fish survive to the following spring and then emigrate to the ocean. In the past several years we have been developing methods to use PIT tags to estimate smolting rate and smolt production in the Carmel River system. Smolts are the immature, saltwater-tolerant form of the fish that migrates down the river corridor to the ocean in late spring. Smolting rate, as used here, is the per-capita rate at which juvenile *O. mykiss* alive at the end of the dry season (September-October) successfully transform into smolts and migrate downstream to the ocean the following spring. Smolt production is an estimate of the annual abundance of smolts, and can be estimated as the product of autumn juvenile abundance (estimated in the last section) and smolting rate, the focus here.

Smolting rate and smolt production are biological indicators that can directly link freshwater habitat condition to expression of anadromy. Once in the ocean, smolts feed and grow and, if they survive, eventually mature into large adult steelhead that return to the river system to spawn. The abundance of returning adults is also a powerful indicator for expression of anadromy. However, it is not as clear an indicator as smolt production for the links between freshwater habitat condition and expression of anadromy, because a substantial and variable amount of mortality can occur in the ocean. Put simply, a low number of adult steelhead does not indicate if the main limiting factor is in the ocean or the river, while low smolt production suggests that there are limitations in the river. High smolt production suggests marine limitations, although smolt condition leaving freshwater can strongly influence marine survival. Finally, a large juvenile abundance combined with a low smolting rate could suggest that the population is dominated by rainbow trout with fewer

steelhead. All this to say that smolt production is a very informative indicator for managing a threatened steelhead population.

PIT-tagging method

Smolt estimation is almost always done using direct capture methods, such as rotary screw traps or fyke nets. While these methods are effective ways to capture smolts and downstream migrants, they do not provide any information about where within the watershed the smolts came from, or any information about which fish did not smolt. This gives these methods limited scope for assessing specific limiting factors or the effect of mitigation measures on smolt production. These methods also provide no way to directly estimate survival from the juvenile to smolt stage. Additionally, you need a large number of smolts captured to measure trap efficiency with catch and release, and it isn't always feasible to capture a large number of smolts (e.g., as was the case in our Los Padres passage study; Boughton et al. 2020).

Because of these data limitations with smolt trapping, we developed and implemented a PIT-tag method for estimating smolting rate in the Carmel River. The PIT-tag method involves implanting PIT tags in juvenile *O. mykiss* captured during the fall population surveys, during summer rescue relocations mitigation, or during opportunistic sampling events, such as lagoon seining. We then use PIT tag antennas to detect the proportion of these fish moving downstream the following spring. Tagged fish from the fall population survey allow us to estimate smolt production for the population as a whole, whereas tagged fish from mitigation actions allow us to estimate the production from the specific mitigation action.

Here we report our first three seasons in which such estimates can be made for the Carmel River. We report preliminary estimates for the smolting rate of in-stream juveniles in the spring of 2018, 2019, and 2020 (i.e., fish that were tagged in fall of 2017, 2018, and 2019), and also the 2019 smolting rate for the juveniles rescued and relocated by MPWMD in the summer of 2018.

We wish to note several limitations to this approach. First, smolting rate as used here includes not just the probability that a juvenile fish transforms to a smolt, but also the probability that it survives the winter months between the time of tagging and the time of migration. In addition, juvenile fish that have not transformed to smolts are also commonly observed to move downstream in the spring; indeed in the heavily studied Scott Creek population of steelhead in Santa Cruz County, juveniles are observed to move both upstream or downstream for significant distances in most months of the year, commonly moving between the estuary and the rest of the river system. The PIT tag

method cannot cleanly discriminate between these ambulatory juveniles and smolts, and thus ‘smolting’ rate can include both categories of fish. To emphasize this point we will instead use the term ‘emigrant rate’. Here we use simple statistical methods to make a preliminary estimate of this emigrant rate, but note that further research may reveal ways to distinguish smolts from migrant juveniles in the tagging data, allowing a more accurate estimation.

A final limitation of the approach is the practical difficulty involved in detecting tagged fish in the river. PIT-tag monitoring stations involve a power source, a streamside box containing the electronics, and one or more large wire-loop antennas deployed directly in the river channel. Tagged fish must come rather close to these antennas to be detected, typically within 20 to 100 cm depending on site conditions, antenna design, and the size of the electronic tag implanted in the fish (12-mm tags are more difficult to detect than 23-mm tags, but are still useful because they can be implanted in smaller fish). Thus, individual antenna are unlikely to detect all the tagged fish passing by them. In addition, PIT tag monitoring stations are vulnerable to a large range of challenges, from ambient electronic noise in the environment interfering with detection, to debris snagging on and destroying antennas, to ghostly electronic failures that defy explanation or troubleshooting but then mysteriously solve themselves.

Thus we expect that imperfect detection of tagged fish is unavoidable in this method. To estimate smolting rate, however, we must be able to estimate the total number of tagged fish that pass by a station, and to get that we must be able to estimate the detection rate of the station. This is typically done by deploying multiple monitoring stations and/or stations with multiple antennas. This redundancy in detection allows us to estimate the detection rates of individual antennas using statistical models known as mark-recapture or mark-resight models.

As a simple example, imagine two adjacent antennas that together detected 100 tagged fish passing by them. Imagine 25 fish were only detected at the first antenna, 25 were only detected at the second antenna, and 50 were detected at both antennas. The fact that some fish were missed by each antenna implies that some unknown number of fish were missed by both, and we need to estimate that number to get our smolting rate. Assuming all 100 fish passed by both antennas, we know the detection rate of each antenna was $50/(25+50) = 0.67$, meaning that each antenna misses $1 - 0.67 = 0.33$ of the tagged fish. Assuming that detection failures are independent across the two antennas, the proportion of tagged fish detected by neither is $0.33 \times 0.33 = 0.11$. Thus the 100 detected fish represent $1 - 0.11 = 0.89$ of the total tagged fish passing by the antenna, implying that the total number was $100/0.89 =$ about 112

fish. If, say, originally 300 fish were tagged upstream of this station than the estimate of the smolting rate is $112/300 = 0.37$. It is possible to use much more sophisticated mark-recapture models accounting for various complications in the data or the assumptions, but this simple example illustrates the essence of the approach. Depending on how we sample the fish to tag and release, we can use this method to estimate overall smolting rate of the population, or we can compare fish tagged and released in different settings to identify specific limiting factors on smolting rate.

Estimates of emigrant rate

For these preliminary estimates we use a simple approach, dividing a small-sample mark-recapture estimator (Thompson 2012, eq. 18.5) by the total number of fish that were tagged upstream of the monitoring station,

$$\hat{s} = \frac{1}{n} \left[\frac{(f+1)(l+1)}{b+1} - 1 \right] \frac{151}{d}, \quad (2)$$

where n is the number of juvenile *O. mykiss* tagged upstream of the monitoring station in the fall or relocated in the summer, and the next three variables (f , l and b) are counts of tagged fish detected emigrating the following spring: f is the total number of tagged fish detected in at the first antenna of the monitoring station, l is the total number detected at the second antenna, and b is the number detected at both. We were not able to keep the stations operational every day of the migration season (151 days from the beginning of January to end of May), so the estimate is expanded from d , the number of days the station operated, to the full 151 days of the season. The underlying assumption is that movement rate did not differ systematically between days the station was operational and days it was not. An approximately unbiased estimator for its standard error is

$$SE = \frac{1}{n} \sqrt{\frac{(f+1)(l+1)(f-b)(l-b)}{(b+1)^2(b+2)} - 1} \left[\frac{151}{d} \right], \quad (3)$$

similarly modified from Thompson (2012, eq. 18.6). This simple approach is limited to the monitoring stations with two antenna sufficiently near one another that the number of fish stopping movement (either settling or dying) between the two antenna is negligible. Ideally this station would be as near the ocean as possible, but unfortunately at neither of the two stations we established near the ocean (between rkm 0 and 10 in Figure 11) were we able to keep two antennas sufficiently functional to make an estimate, due to the

instability of the stream bed and the large amount of floating woody debris that gets mobilized during higher flows and snags on the antenna. However, in 2018 and 2019, the next two stations upstream, established by MPWMD, were significantly more robust and could maintain two operational antennas for the peak of the smolt season in April and May in both years. In 2020, another paired MPMWD antenna at Rancho San Carlos was able to maintain two operational antennas for Most of January-May.

These stations (Sleepy Hollow station near rkm 28 in Figure 11, Scarlett station near rkm 15, and Rancho San Carlos near rkm 5.6) were still subject to failure, especially in January and February of 2019. A test of the data showed that at all stations except for Scarlett in spring 2019, the days in which one of the antennas was failing were independent of the days in which the other antenna was failing. This independence of detection failure is an assumption of the estimator (Eq. 1). The Scarlett station in spring 2019 showed that both antennas tended to be non-functional on the same day, 2.6 times more often than expected by random chance. This will tend to negatively bias the estimate of emigrant rate for that station in 2019.

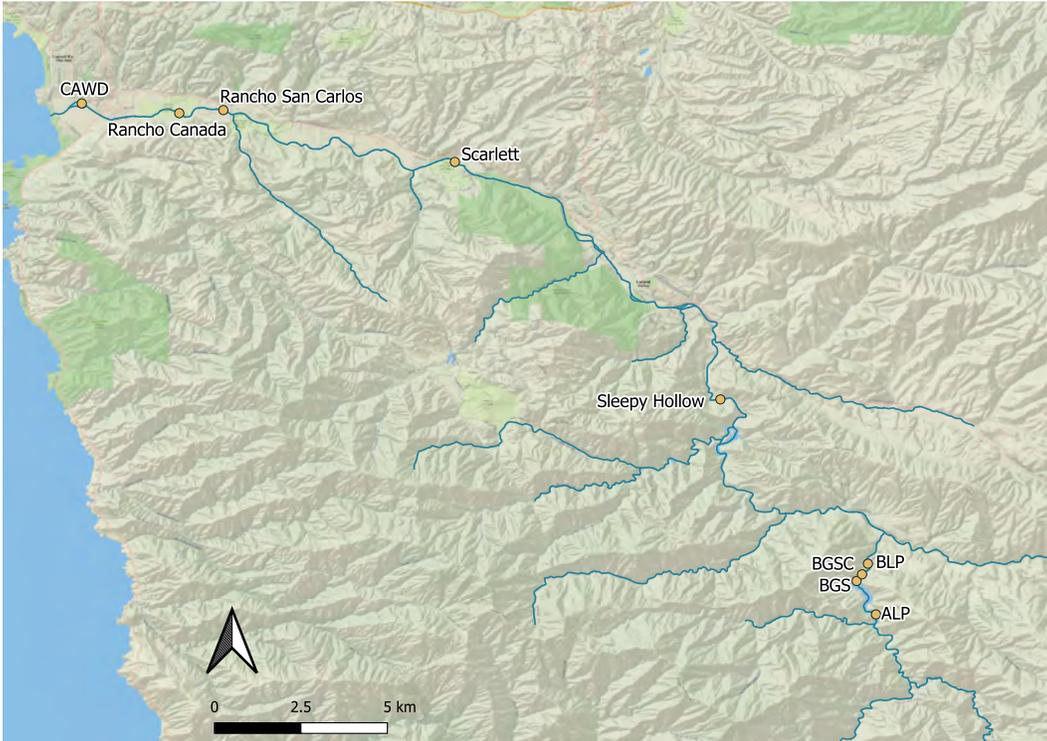


Figure 11: PIT tag antenna locations in the Carmel River. Not all antennas were operational from 2017-present. The CAWD site was retired in 2019 because of maintenance issues from to high sand transport in the lower river.

The estimates for emigrant rate (Table 7) ranged from 0.031 to 0.15 depending on tag size, year, and origin of fish (instream versus relocated). Estimates for relocated fish moving past Sleepy Hollow in 2019 and Rancho San Carlos in 2020 could not be made due to too few fish detected at each antenna, which prevents an estimate of detection rate. For the other estimates, most had a coefficient of variation (CV, the standard error scaled by the estimate) of 16% or less, which is rather good precision. One had CV of 25% and the worst was 36%.

Figure 12 graphs these emigrant rates with 95% confidence intervals. The small tags (12 mm) were implanted juveniles with fork length (FL) 65 – 99 mm at the time of tagging, while the large tags were implanted in individuals with FL > 100 mm. Those with FL < 65 mm were too small to tag. Given that larger juveniles are more likely to transform to smolts, and should have higher fall-spring survival, the higher emigrant rate for in-stream fish with large tags is not surprising. The in-stream fish with smaller tags had emigrant rates that were lower and more variable, likely reflecting the lower survival

and emigration rate of smaller juveniles.

A noticeable difference in the 2020 estimate made at the Rancho San Carlos antenna is that the emigration rate estimates were lower and had tighter confidence intervals. The narrower confidence intervals reflects the high detection probability at that antenna (i.e., fish detected at one antenna were very likely to be detected at the second). The lower emigration rate estimates could be either because smolting rate was lower in 2020 than the previous two years, or it was about the same but the earlier estimates missed some substantial mortality occurring in the lower river between the Scarlett and RSC stations. If there is mortality during the downstream migration from Sleepy Hollow and/or Scarlett to Rancho San Carlos, the estimate at Rancho San Carlos would be lower, as observed. We will analyze these alternatives further in future analyses.

The relocated fish in 2019 had emigrant rates of about 8% at the Scarlett station, regardless of tag size. For the larger fish that had been implanted with large tags (23 mm), this rate was about half the emigrant rate of in-stream fish. In the two bottom panels of Figure 12, one can see that the 95% confidence intervals for in-stream fish and relocated fish do not overlap vertically, indicating that this difference is statistically significant. It is important to note that the rescues would be expected to have slightly lower rate because they include an additional 3-4 months between the time of tagging and the time of migration, increasing their exposure to mortality.

Table 7: Per-capita emigrant rates of *O. mykiss*, estimated from PIT tags. n is the number of *O. mykiss* tagged or relocated upstream of the station. f, l, b are the total number of unique tags detected between 1 January and 31 May at the first antenna, last antenna, and both antennas, respectively. d is the number of days between 1 Jan and 31 May the station was operational.

Station Name	Tag Size	Tagged Fish Counts					Emigrant Rate ¹		
		n	f	l	b	d	s	s.se	CV
2018 In-Stream Fish									
Scarlett	12mm	1007	23	23	12	139	0.0467	0.0059	13%
Sleepy Hollow	12mm	656	25	14	10	92	0.0862	0.01	12%
Scarlett	23mm	785	53	54	29	139	0.1356	0.0111	8%
Sleepy Hollow	23mm	514	35	31	23	92	0.1501	0.0088	6%
2019 In-Stream Fish									
Scarlett	12mm	1031	30	13	8	99	0.0699	0.0114	16%
Sleepy Hollow	12mm	581	5	3	1	69	0.0414	0.0151	36%
Scarlett	23mm	476	28	19	11	99	0.1517	0.0208	14%
Sleepy Hollow	23mm	313	9	14	6	69	0.1428	0.0212	15%
2020 In-Stream Fish									
Rancho San Carlos	12mm	2030	35	38	21	149	0.0314	0.0027	9%
Rancho San Carlos	23mm	436	33	37	27	149	0.105	0.0043	4%
2019 Relocated Fish									
Scarlett	12mm	583	15	9	4	99	0.0811	0.02	25%
Sleepy Hollow	12mm	124	1	0	0	69	-	-	-
Scarlett	23mm	1321	52	19	14	99	0.0804	0.0086	11%
Sleepy Hollow	23mm	194	1	1	0	69	-	-	-
2020 Relocated Fish									
Rancho San Carlos	12mm	352	4	0	2	149	-	-	-
Rancho San Carlos	23mm	26	1	0	1	149	-	-	-

¹ Includes mortality between time of tagging and detection at station.

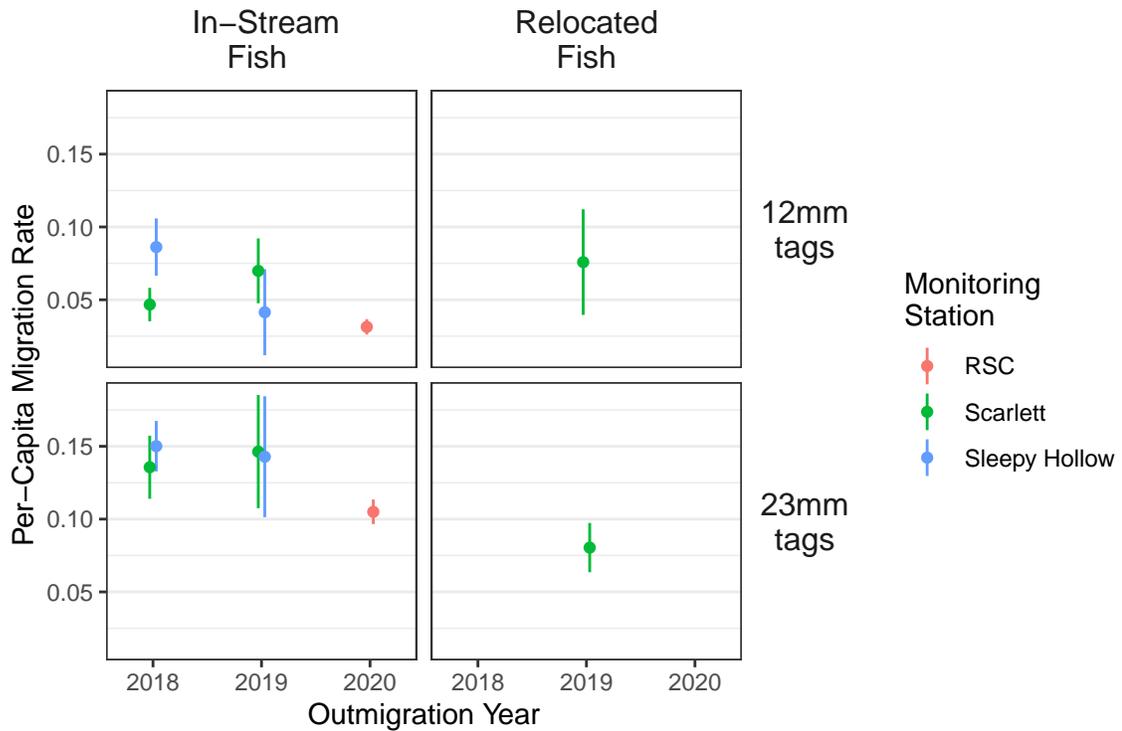


Figure 12: The tagged and relocated rescues in our dataset were primarily from the 2018 rescue season. Nearly all of the relocated rescues were captured from June-August.

Overall, we conclude that the PIT tagging method can be used to estimate smolting rates with precision and provide key information on population performance that cannot be obtained otherwise. Maintaining the operation of PIT tag antennas is a challenge, although our flexible-pass-through design has proved more robust and agile than other designs. Still, failure of antennas in response to river conditions is inevitable and will require development of more sophisticated statistical methods to account for non-independence in the failure events of individual antennas. The precision of the estimates of smolting rate will often be high enough to have statistical power to compare different groups of fish. However, operational constraints (release dates for tagged fish, siting of PIT tag stations in the river channel) may cause ambiguities in interpretation, because some release groups may be exposed to mortality risks for a longer time than others. Our estimates of smolting rate were generally low ($\leq 15\%$) and appear to have substantial scope for improvement.

6 Movement patterns

Understanding when and where fish are moving within the Carmel River is at the foundation of understanding the Carmel steelhead population and its status. The timing and amount of movement gives us information about what habitats are important and the seasonality of that importance, what conditions may limit movement, and when river connectivity is especially important. In the Carmel some particular questions are: In what seasons do we see movement into or out of the lagoon, do the low flow conditions of summer limit movement, and in what season do we observe peak downstream migration of juveniles and smolts?

Our extensive PIT tagging and widespread antenna locations allow us to examine these questions among several different categories of fish. Here we report qualitative and preliminary results on the movement patterns of fish tagged during fall population surveys, summer rescue relocations, a single summer lagoon survey, and lastly, we examine fish that did not move, but were instead detected at a single location over an extended period of time.

All fish larger than 65 mm FL are tagged with PIT tags during all fall and summer capture events. Fish that are 65-100 mm FL are tagged with 12-mm PIT tags, and fish larger than 100 mm FL are tagged with 23-mm PIT tags. The movement patterns were analyzed separately for the 23- and 12-mm PIT tags because we predicted different movement patterns between smaller and larger fish, and because 23-mm PIT tags have greater detection distances at the antennas.

To characterize movement patterns, we calculated the total number of detections by month separately for fall survey and rescue relocation fish, and categorized the direction of movement leading up to that detection. A downstream movement occurred when the previous detection (either at the tagging location or at an antenna) was upstream of the detection. An upstream movement occurred when the previous detection was downstream of the antenna detection. A ‘stationary’ detection was when the previous antenna detection occurred at the same antenna as the focal detection. Repeat detections at an antenna were filtered by day. For example, a fish detected 100 times at the Sleepy Hollow antenna in a single day would only count as one detection in this movement summary. Additionally, the three antenna sites with paired antennas (i.e., Sleepy Hollow, Scarlett, Rancho San Carlos) were filtered such that a fish detected at both paired antennas in a single day was counted as only one detection. This filtering by day and within paired antenna sites prevented an exaggeration of stationary movement points.

Movement patterns of fish tagged during fall population surveys

A total of 8,554 juvenile steelhead have been PIT tagged during fall surveys in September and October from 2017-2021. Note that because this analysis was done in early March of 2021, the movement patterns do not include any spring movements of fish tagged in the fall of 2020.

We expected to see a peak in downstream movement during spring (March-May), and indeed, the movement data support this expectation. It is notable that the timing of peak downstream movement varies by fish size (and tag size). In fish larger than 100 mm, we observed the highest number of downstream movements in March, followed by a high number in April (Figure 13). In fish smaller than 100 mm (and larger than 65 mm), we observed high numbers of downstream movements in March and April, but the highest numbers occurred in February and May (Figure 13). The patterns observed in the different size categories suggest that smaller fish move downstream (either to smolt or rear in the lower river or lagoon) at the early and later tails of the smolt season, whereas larger fish move downstream primarily during the ‘typical’ smolt season in March and April. By June downstream movements in both tag sizes had declined significantly, which suggests that downstream emigration (by smolts or juveniles) was completed by June.

We anticipated that all movements (upstream, downstream, and stationary) would be lowest during the low flow months of June to October because river connectivity decreases, water temperatures are at their highest, and growth is at its lowest, and therefore fish would adopt low-movement behaviors that conserve energy. This is mostly the pattern we observed in the fish larger than 100 mm, although there was a slight increase in upstream movement in September (Figure 13). However, this was not the pattern we observed in the fish smaller than 100 mm. In the smaller fish, we observed upstream movement in August-October, followed by a significant increase in upstream movement in November and December. Upstream movement in the larger fish also peaked in December.

Stationary movements, or repeated daily detections at a single antenna site, were the most common detections we observed in both tag sizes (Figure 13). Stationary movements could be either short-term or long-term milling at a site or longer back-and-forth movements that are smaller than the next closest antenna. In fish less than 100 mm, stationary movements were high from January to May, lowest from June to October, and peaked in December. This general pattern was true for large tagged fish as well, however the overall number of stationary detections was less. The peak stationary movement

in November and December suggests that decreased water temperatures and slightly elevated flows in the late fall and early winter may spur in-stream movement. However, this may also be an artifact of the high number of tags released during the fall survey in September - October, combined with tag attrition as time passes.

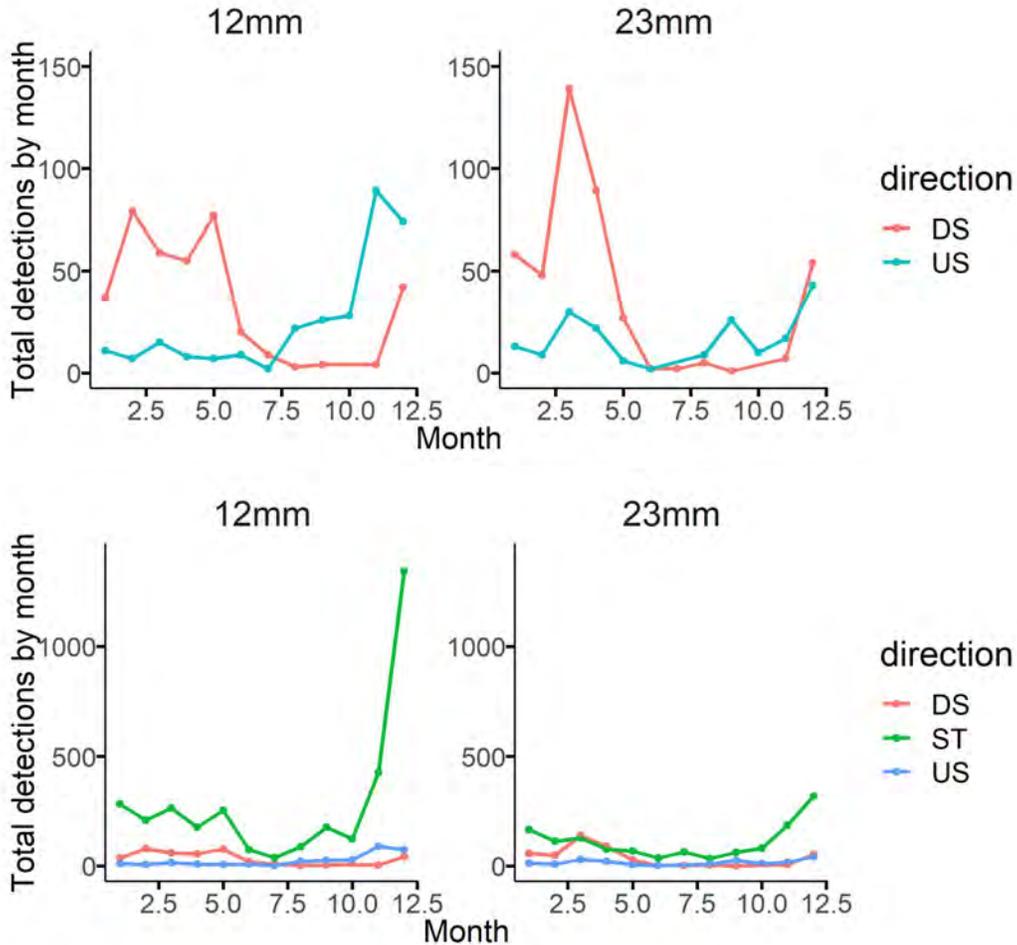


Figure 13: Monthly movement patterns of fish tagged during fall population surveys. Downstream (DS), upstream (US), and stationary (ST) movements were tallied by month and plotted separately for large (23 mm) and small (12 mm) tags. We excluded stationary movements from the top plots to improve the visibility of the upstream and downstream movement patterns.

Movement patterns for fish tagged during summer rescue relocations

One of the mitigation actions of the last three decades has been relocations of by MPWMD from drying stream sections to sections with adequate flow. We can use PIT tags to examine the movement patterns of these fish. Most relocated rescues were captured (rescued) in July and August (Figure 14). The mainstem relocated rescues were released upstream of their capture location, whereas the tributary relocated rescues were released downstream at the mainstem confluence of their respective tributaries. The first observed movements were measured from the release site and not the capture site (subsequent observed movements were measured from the previous antenna detection site).

We hypothesized that relocated rescued fish would follow similar movement patterns to fish tagged in the fall, such that there would be a peak of downstream movement during spring smolt season and few movements during the summer low flow season. Contrary to our hypothesis, peak movement occurred in July, although the movement direction differed by fish (and tag) size category (Figure 15). The fish with 12-mm tags (<100 FL) were more likely to move downstream in July, while the fish with the 23-mm tags (>100 FL) were more likely to move upstream (Figure 15). Directional movement decreased through the summer, but stationary movements remained high. This pattern was observed in both tag sizes, and was of similar magnitude to the detections we observed in July. There were a high number of stationary movements (repeated daily detections at the same antenna site) from July to February, with a peak in August for both tag types.

One hypothesis for the high number of directional movements in July observed in relocated fish is that fish relocated during the low flow (and low movement) season must find a new feeding territory. If all of the feeding territories are occupied in the reach where they are released, they must move in search of a territory. The movement direction difference between small and large fish after translocation is interesting and suggests that movement behaviors may be driven, in part, by fish size.

Notably, there was very little downstream movement observed from March-May, which is when we observed peak downstream movement in fall tagged fish and is the ‘typical’ smolt season. Most downstream movement instead took place from November-January in both tag sizes. One explanation for this movement is that if relocated rescues struggled to acquire feeding territories during the summer and fall, they may be more likely to migrate downstream in the early winter once flows increase and the river re-connects with the lagoon. The lagoon has the potential to provide considerable growth opportunities,

and it may be that an adaptive strategy for this steelhead population (and others in California) is for less competitive individuals, such as individuals without territories, to migrate downstream to the lagoon in hopes of growing big before smolting. We did not observe a fall-early winter downstream migration pattern in the fall tagged fish, however if this downstream migration only occurs in a small fraction of fish, it would be difficult to detect. By tagging the relocated rescues we may have inadvertently targeted those less competitive (no territory) individuals, which gave us higher resolution to detect this pattern. The downstream movements observed during November-January may also explain why we did not observe as much spring smolt movement, because many of the relocated rescues have already entered the lagoon prior to the smolt season.

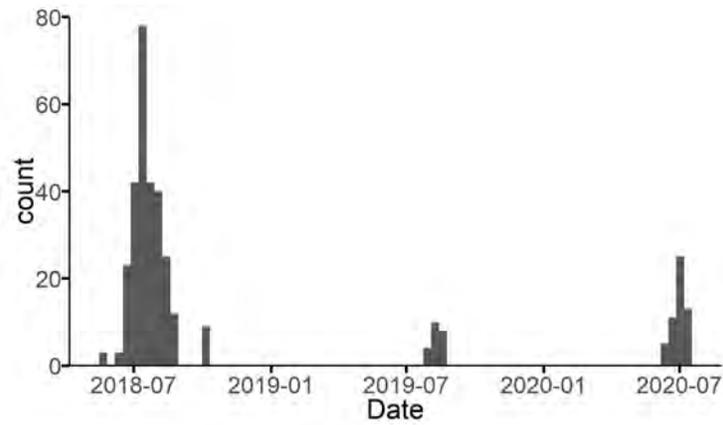


Figure 14: The tagged and relocated rescues in our dataset were primarily from the 2018 rescue season. Nearly all of the relocated rescues were captured from June-August.

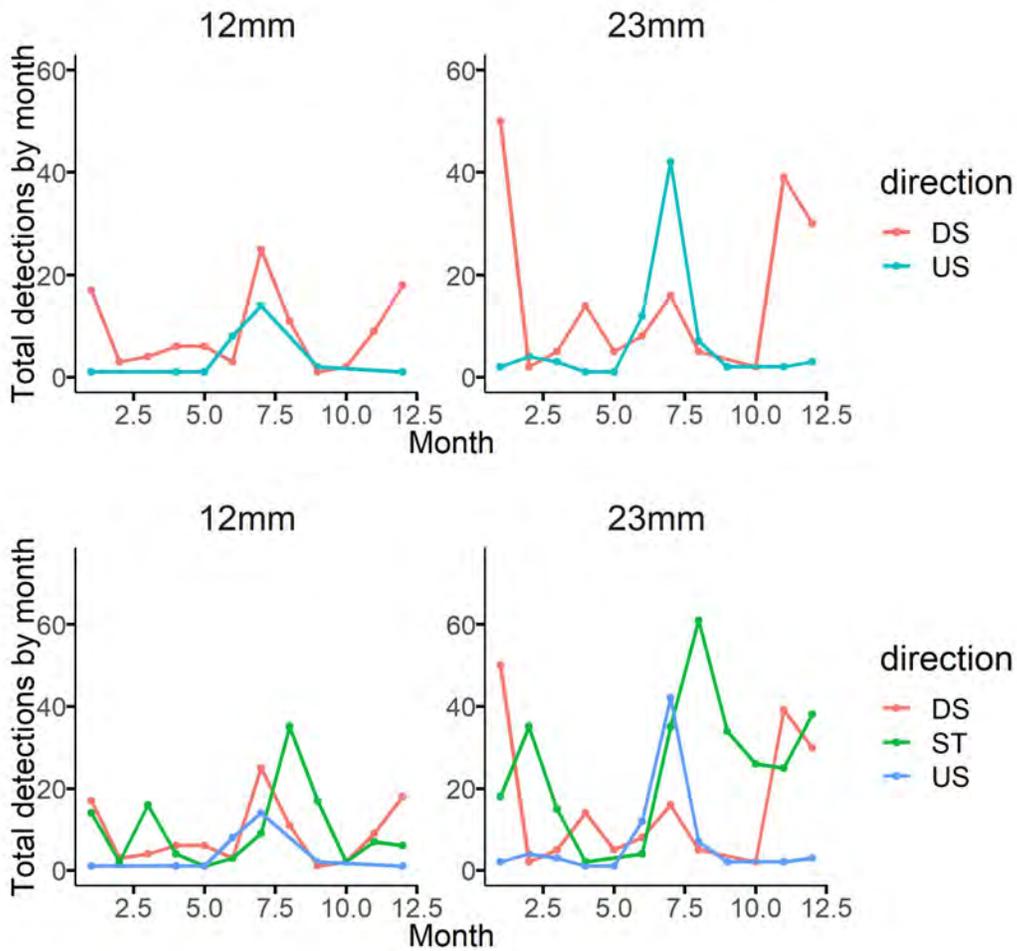


Figure 15: Monthly movement patterns of fish tagged during spring and summer relocation rescues. Most fish were tagged during 2018 from June-August. Relocated rescues were collected in the lower Carmel River mainstem, Cachagua tributary, Potrero Creek, Garzas Creek, and Hitchcock Creek. Downstream (DS), upstream (US), and stationary (ST) movements were tallied by month and plotted separately for large (23 mm) and small (12 mm) tags. We excluded stationary movements from the top plots to improve the visibility of the upstream and downstream movement patterns.

Overall, these preliminary analyses suggest that summer-relocated rescues have different movement patterns compared with fall-tagged fish. Fall-tagged fish showed peak downstream movements in March-May, and low summer movement. Summer-relocated rescues showed significant summer movements

and earlier downstream movements in November-January, compared with fall-tagged fish. The downstream movements combined were over a longer period than we expected, and suggest that river-lagoon connectivity from November-May may be especially important for the population.

Lagoon movements

Research in Scott Creek, California has established that intermittent estuaries (i.e., lagoons) can be especially important rearing habitats for juvenile steelhead and coho salmon, and that lagoon-reared fish can make up nearly all (87-96%) of returning adult steelhead in some years (Bond et al. 2008). Growth opportunities in lagoons can be very high during summer when the rest of the watershed has limited growth opportunities (Hayes et al. 2008). Small spring emigrants have been observed moving into lagoons during spring, doubling in size during the summer, and then either smolting or returning to the stream (Bond et al. 2008; Osterback et al. 2018). Even though the Scott Creek lagoon represents only 5% of the watershed area, it plays an outsized role in the population carrying capacity and overall dynamics.

The role of the Carmel River lagoon as rearing habitat was examined by Dettman (Dettman and Kelley 1986). They seined the lagoon on 11 occasions between April-October in 1982. All fish they captured from late April-early June were age-1 and the majority had smolt characteristics. They attempted to mark and recapture individuals to estimate smolt residence time in the lagoon, however they were only able to recapture three individuals. These three had spent 11-17 days in the lagoon, and from these results they concluded that smolts spend relatively little time in the lagoon before migrating to the ocean.

By early July, Dettman and Kelley (1986) began to capture far fewer age-1 juveniles and more YOY. YOY captures were highest in late August when they captured approximately 1,500 YOY in a single seine haul. Their last seining event was in mid-October and they caught no fish in two seine hauls. They observed that food was quite abundant during the summer, but that the food in stomachs was very low. They also observed significant predation on steelhead YOY from terns and pelicans, and estimated that 2,000-3,000 YOY per month could be consumed by bird predators. They did not measure individual fish growth in the lagoon or examine movements out of the lagoon.

Although steelhead use of the lagoon was not part of our planned study, we took the opportunity to PIT tag fish as part of a lagoon rearing estimate planned by the Carmel River Steelhead Association and MPWMD. In 2019 we PIT tagged 138 juvenile steelhead that were captured via seine net in the Carmel River lagoon and used our existing PIT antenna infrastructure

to estimate movement timing out of the lagoon. The capture and tagging took place on July 27, 28, and 30, 2019 in collaboration with Carmel River Steelhead Association and MPWMD. The fish were larger than the fish we typically capture during the fall surveys, with a mean size of 162 mm FL (size range 99-275 mm FL).

Of the 138 tagged fish, we subsequently detected 16 of those fish at our upstream antennas. One of those fish was detected on August 1-2 at the Rancho San Carlos antenna. The remaining fifteen were detected moving upstream between December 4-10, 2019, which was 2-8 days after a large rainstorm re-connected the river on December 2 (Figure 16). Two of those 15 were detected moving as far upstream as the Sleepy Hollow antenna, and they did so quickly, reaching that antenna by December 11 and 13. Ten of the 15 were detected moving back downstream during smolt season, between January 12-May 18, 2020. Remarkably, one of the fish detected moving back downstream in January of 2020 returned to the river the following year, presumably as an adult spawner, and was detected at the Rancho San Carlos antenna on January 29, 2021. It continued traveling upstream to the Below Los Padres antenna where it was repeatedly detected from January 5-March 5, 2021. It then returned downstream, presumably as a kelt, and was detected the Rancho Canada antenna on April 2, 2021.

Information about summer lagoon rearing was further bolstered by a fish that MPWMD rescued, relocated, and tagged on July 8, 2020 in the lower mainstem Carmel River. MPWMD relocated it to site 79, approximately 20 km upstream from the lagoon. This fish moved back downstream on July 17, 2020 and was detected at the Rancho Canada (Palo Corona) antenna, which is our antenna furthest downstream. This fish presumably remained in the lagoon until we detected it again moving upstream, first on December 17, 2020, at the Palo Corona antenna and then on December 18, 2020, at Rancho San Carlos. This fish remained in the river upstream of Rancho San Carlos for two months before being detected again at Rancho San Carlos on February 1 and February 4, 2021.

Although our sample sizes of juvenile PIT tagged steelhead in the lagoon are quite small, they provided useful insight nonetheless. We conclude that at least some juvenile *O. mykiss* are successfully using the lagoon habitat for summer rearing, despite the presence of striped bass. We still do not know what impact bass predation has on juvenile steelhead. The summer lagoon rearing, followed by smolting in the spring and high ocean survival, is a life history pattern that has also been observed in Scott Creek and supports the hypothesis that lagoons are important habitats for central coastal steelhead populations.

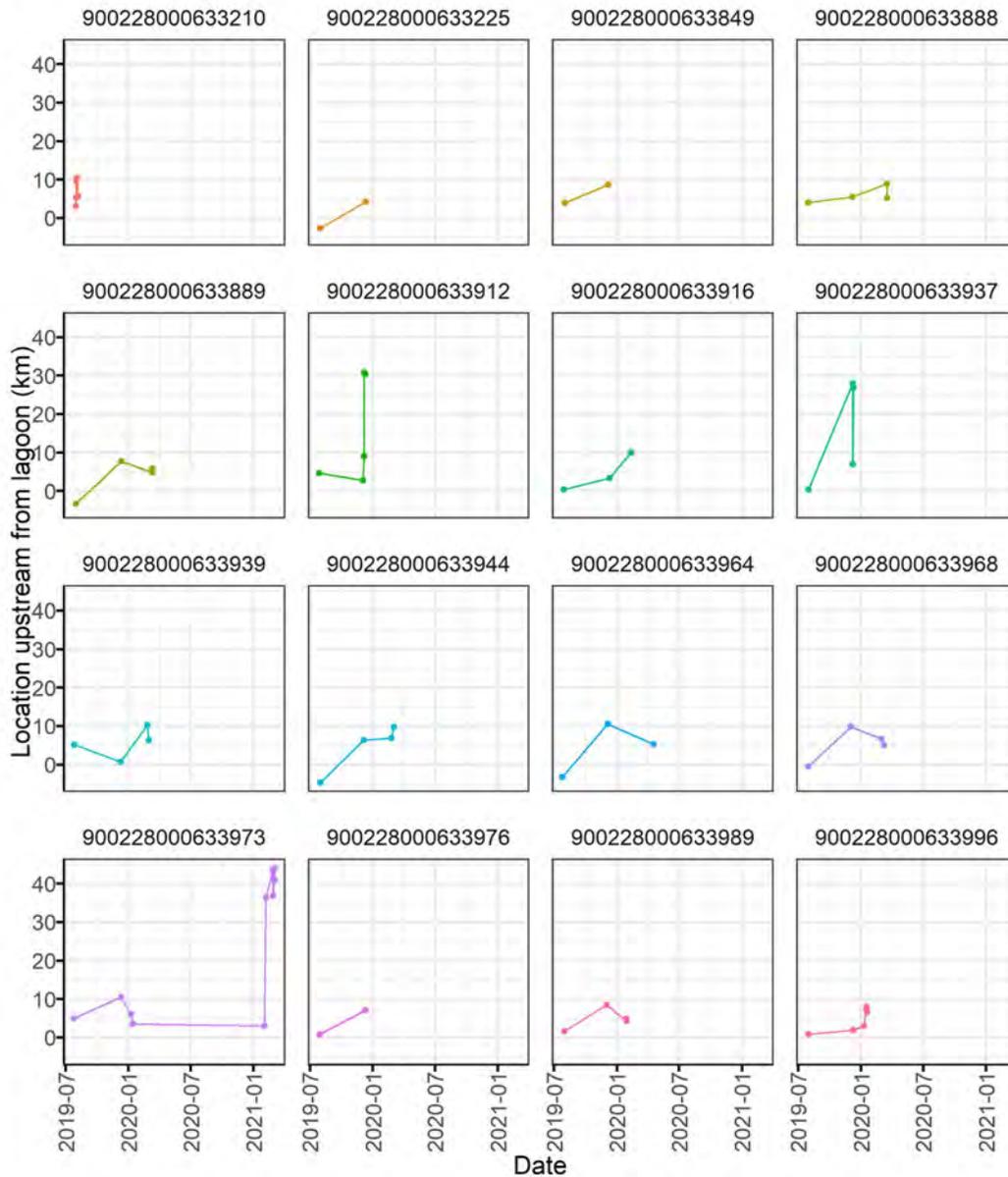


Figure 16: Movement patterns of the 16 fish tagged in the lagoon in July 2019 and detected in the river. Each point represents a daily detection (either a single detection or multiple within a single day) at one of our PIT tag antennas. The antennas are arranged by their distance upstream from the lagoon. For reference, the Rancho San Carlos antenna is located 5.6 km upstream of the lagoon, the Sleepy Hollow antenna is located 28.5 km upstream of the lagoon, and the Below Los Padres antenna is located 41 km upstream of the lagoon.

Stationary fish

Movement patterns can tell us a lot about how fish use habitat, but equally as important are the fish that do not move. For example, it may be that only a small fraction of tagged fish follows the above movement patterns while the others remain in the habitat where they were tagged. The lack of movement is often more difficult to observe because fish are only detected when they swim past our antennas. However, we have observed that some fish are present near the antennas for extended periods of time, so we decided to examine the characteristics of those fish specifically.

To identify ‘stationary fish’, we filtered the data for fish that were detected for at least 50 days over a period of 100 days or more. Forty-two fish met these criteria. Forty-one were tagged during fall population surveys and one was tagged as a relocated rescue. Most (36) were repeatedly detected at the Sleepy Hollow antennas, and the remaining 6 were repeatedly detected at the Scarlett antennas (Figure 17). All but two fish were tagged at sites within 0.5 km of the antenna at which they were detected.

Our antenna operation periods heavily influence the months that we observed repeated detections (Figure 17). We did not operate the Sleepy Hollow or Scarlett antennas during the summer in 2018 or 2019, however we can infer from four fish that were present in both spring and fall at Sleepy Hollow in 2019 that some fish remained at the antenna over summer. We observed the highest frequency of repeat detections from January to June. This timing overlaps with the highest frequency of directional movements (Figure 13), and indicated that although many fish move during the high flow season, others do not move long distances and continue to hold territories through the high flow season.

The size range of stationary fish detected over 100 days was 67-229 mm FL, which is very similar to the overall size range of all fish we tagged during fall surveys (65-420 mm FL). These fish were likely a mix of resident rainbow trout and juveniles that have not yet smolted. The fish with the longest duration at Sleepy Hollow (from fall of 2018 to summer 2020) was 226 mm FL at the time of tagging and was likely a resident rainbow trout (Figure 18). Fish in the 67-100 mm FL size range that were detected for shorter durations are likely juvenile steelhead.

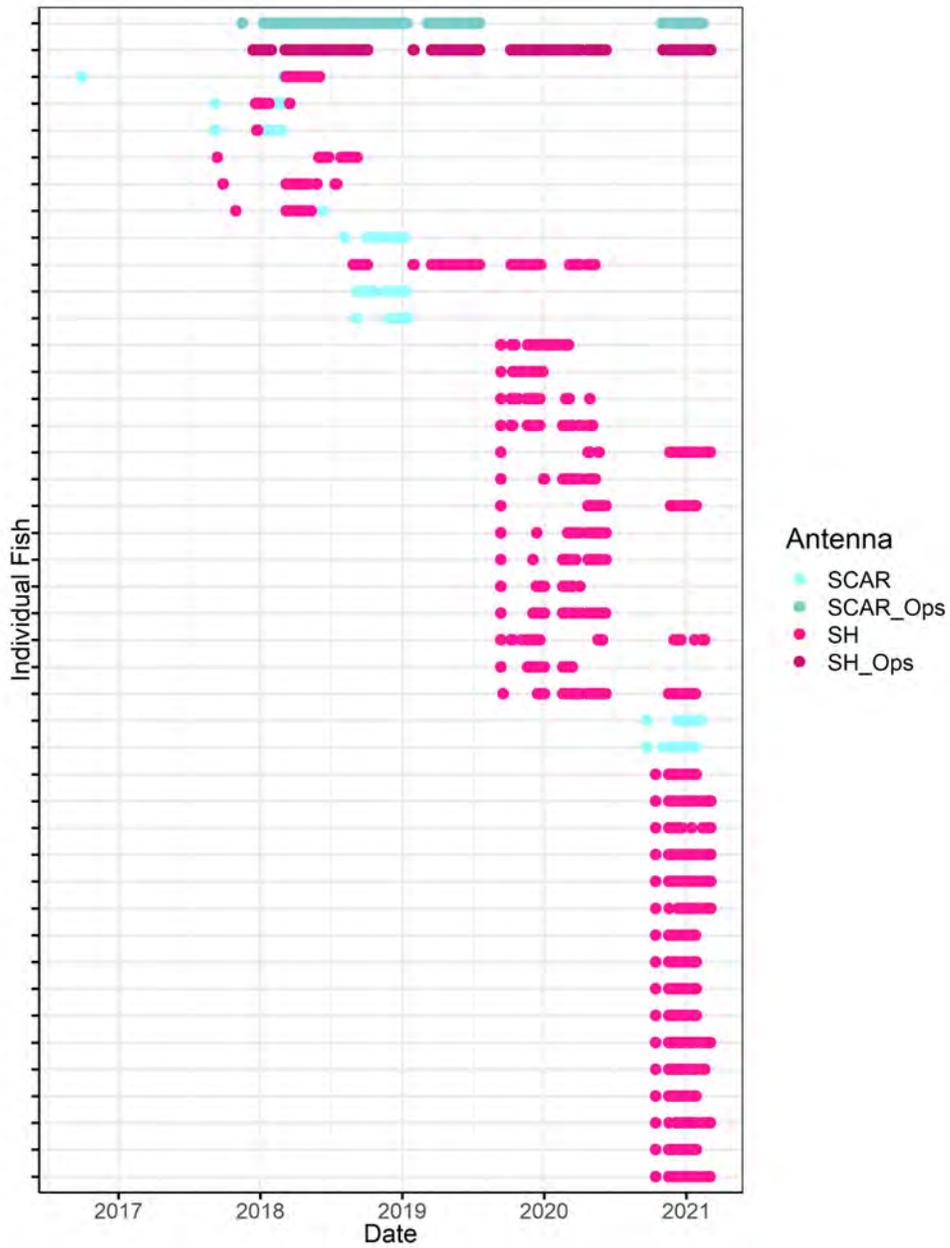


Figure 17: Between 2017 to March 5, 2021, 42 fish tagged during fall surveys were detected for 100 days or more. Thirty-six of these fish were detected at the Sleepy Hollow (SH) antenna and 6 were detected at the Scarlett antenna (SCAR). The operation periods of each antenna (SCAR_Ops, SH_Ops) are shown in the first two rows of the plot. The first point for each fish represents when they were tagged. All but two fish were tagged at sites within 0.5 km of the antenna at which they were detected.

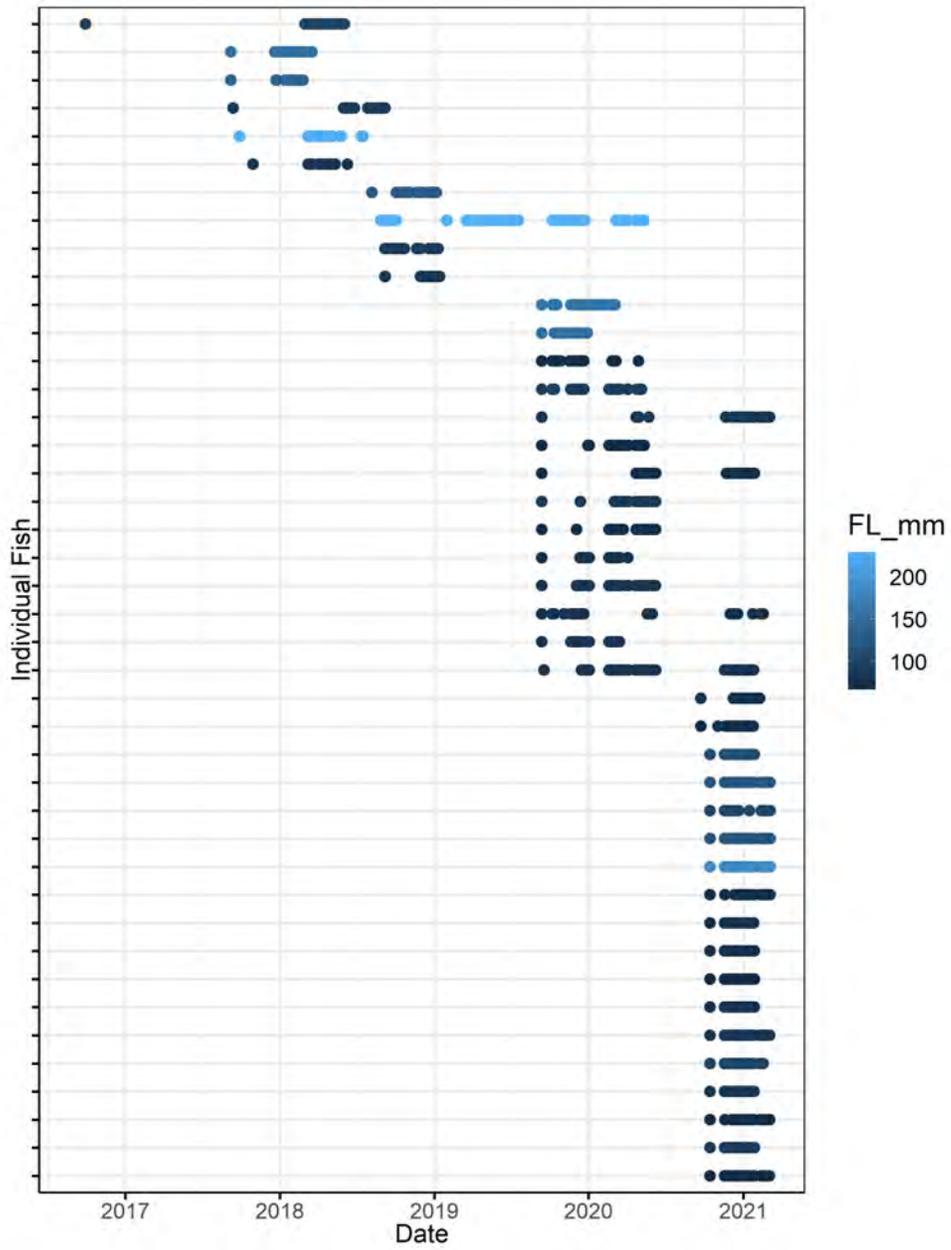


Figure 18: Sizes of the 42 'stationary fish' detected between 2017-March 5, 2021.

Movement summary

We observed quite different movement patterns between fall tagged fish and relocated rescues. Fish tagged in the fall show relatively little movement until November, when temperatures have cooled and flows have come up. There is not a dominant movement direction at this time. However, once February arrives there is a strong downstream movement pattern among smaller fish (<100 mm FL) and that continues through May. Larger fish (>100 mm FL) move downstream in high numbers in March and April. This pattern is typical of a spring smolt outmigration period. After May, movement declines to almost zero and remains that way through the dry season.

Rescued and relocated fish show a considerably different movement pattern. Rescued fish are relocated in July and are very mobile during that month, when non-rescued fish are not. Larger fish are predominantly moving upstream whereas smaller fish are slightly more likely to move downstream. After that initial movement, directional movements decrease but stationary movement stays relatively high though the dry summer and fall compared with the non-rescued fish. In November there is a pulse of downstream movement that continues through January. However, movement stops after January, which is strange because that is when non-rescued fish begin their downstream migration. We hypothesize that much of the unique movement pattern among the rescued fish can be explained by their relocation and subsequent loss of territory or status. When fish are relocated during summer, they initially move around looking for a new territory in which to over-summer. As a newcomer they do not find a good territory or end up as a subdominant fish, so when water comes up and conditions cool off, they move downstream in hopes of reaching the lagoon or newly open lower river habitat.

We know that some fish do make it to the lagoon and over-summer there because of the fish we captured in 2019 and the MPWMD rescue detection. The fish we tagged in the lagoon moved upstream immediately after the first winter rainstorm in December, which is a pattern consistent with high movements in fall and rescue tagged fish. Taken together these movement patterns and differences suggest a couple of things. The lagoon is an important rearing habitat, especially for non-dominant fish and should be considered an important contributor to the overall carrying capacity of the watershed. Non-dominant fish are not limited to rescues, rather they are part of a natural hierarchical system that exists within this territorial species and the lagoon provides habitat for these individuals to grow and contribute to the population. Additionally, early winter appears to be an important movement period, and exceptionally low flow years likely limit connectivity and growth opportunities more than

previously appreciated.

7 Tagged juveniles returning to spawn

In the same way that smolting rate can provide information about survival during the freshwater stage, smolt-to-adult return rates can provide information about survival during the marine stage. We had hoped to use our PIT tagged fish to estimate smolt-to-adult survival patterns, however we were not sure if we would have a large enough sample size to make those estimates. Preliminary spawner data suggests that we will be able to estimate smolt-to-adult in future analyses.

As of April 10, 2021, we have observed 27 fish that were tagged as juveniles and returned as adult spawners three or more years later (Table 8). Two of these fish were captively reared and released from the MPWMD Sleepy Hollow Rearing Facility (one in 2013 and the other in 2016). Six of these fish were rescues that were relocated from the lower mainstem Carmel River in 2018. The remaining 19 were tagged during fall population surveys from 2015-2019.

We identified these returning spawners by filtering the PIT tag antenna data for detections that occurred from January-May three or more years after tagging. We excluded fish detected two years after tagging from this table because of our difficulty in discerning between fish that smolted compared with fish that spawned two years after tagging. We are currently working on methods to identify two year spawners and smolts, and will update this spawner table with those results in the future. Only two fish were detected returning more than three years after tagging (Table 8). One was a fish reared and released from NOAA SWFSC in 2013 returned five years after tagging, and was possibly a returning kelt given its age. The other was a juvenile tagged at Garland Park in 2016 that returned to spawn four years later in 2020. One tagged recapture at the adult weir in 2021 returned two years after tagging.

We detected smolt movements (downstream movement patterns from February-May) in seven of the returning tagged fish. Five of these fish smolted in the first spring after tagging and spent two years in the ocean, while the other two fish smolted two years after tagging and spent only one year in the ocean. This pattern is consistent with steelhead age data from California (Busby et al. 1996), as well as Dettman and Kelley (1986) Carmel River study. It also highlights that there are juveniles that smolt two years after tagging and we need to find a method to identify those cases. Overall, we conclude that smolt-to-adult survival estimates will likely be possible in at least some study years.

Table 8: Juvenile fish tagged during captive rescues (Cap), relocation rescues (Relo), fall surveys (Fall), and Los Padres passage study (LP) that returned as adults based on antenna detections and weir capture.

Event	PIT Tag	FL (mm)	Wt (g)	Tag Size (mm)	Category	Date	Site
Cap	000000179228693	187	67.6	23	Tag	12/2/2013	SHSRF, SWFSC
					Spawn	1/22/2018	RSC
					Kelt	3/22/2018	RSC
Cap	982000362714457	148	33.1	23	Tag	8/24/2016	SHSRF-QT-5
					Spawn	1/8/2019	RSCDS, RSCUS
Relo	900226000593301	92	11.3	12	Tag	7/9/2018	Lower MS
					Spawn	4/3/2021	RC
Relo	900226000593460	175	65.1	12	Tag	7/2/2018	Lower MS
					Spawn	2/1/2021	RSC
Relo	900226000593475	98	10.4	12	Tag	7/3/2018	Lower MS
					Spawn	2/4/2021	RSC
Relo	900228000631926	169	52.5	23	Tag	7/25/2018	Lower MS
					Smolt	3/19/2019	Scar2
					Spawn	1/30/2021	RSC
					Spawn	2/15/2021	SH2
					Spawn	2/25-3/6/2021	BLP
Relo	982000365198736	90	7.1	12	Tag	8/6/2018	Lower MS
					Move?	12/18/2018	Scar1
					Move?	5/30/2019	ScarUS
					Move?	6/4/2019	SH2
					Smolt	3/2/2020	RSCDS

Table 8 – continued from previous page

Event	PIT Tag	FL (mm)	Wt (g)	Tag Size (mm)	Category	Date	Site
					Spawn	3/12/2021	Weir
					Spawn	3/15/2021	RC
Relo	982126054219046	101	11.3	23	Tag	10/3/2018	Lower MS
					Spawn	3/30/2021	RC
Fall	900226000324925	76	5.1	12	Tag	10/10/2018	92
					Spawn	1/28/2021	RSC
Fall	900226000325151	90	8.4	12	Tag	9/24/2018	121
		510			Spawn	3/12/2021	Weir
					Spawn	3/12/2021	RC
Fall	900226000593922	76	5.7	12	Tag	10/20/2016	SCR Upper
					Smolt	3/12/2018	SH1
					Spawn	1/8/2019	Scar1, Scar2
Fall	900226000594292	92	8.9	12	Tag	10/9/2015	SCR Upper
					Spawn	4/5/2018	SH1, SH2
Fall	900226000594323	79	5.9	12	Tag	10/9/2015	SCR Upper
					Spawn	3/13/2018	SH1
					Spawn	3/14/2018	SH1
Fall	900226000594528	95	10.5	12	Tag	9/26/2016	Garland
					Spawn	2/9/2020	RSCDS
Fall	900228000593559	148	37.6	23	Tag	11/2/2017	122
					Smolt	3/30/2018	RSC
					Spawn	2/6/2020	RSCDS
					Spawn	2/23/2020	SH2, SHUS

Table 8 – continued from previous page

Event	PIT Tag	FL (mm)	Wt (g)	Tag Size (mm)	Category	Date	Site
					Spawn	3/1-3/2/2020	SH2
Fall	900228000634137	153	40.8	23	Tag	8/30/2018	43
					Spawn	1/30/2021	RSC
					Spawn	2/11/2021	BLP
					Kelt?	3/19/2021	RC
Fall	900228000689303	31.8		23	Tag	10/6/2019	Valley Green
		500			Spawn	2/18/2021	Weir
Fall	982000362714163	201	88.3	23	Tag	9/22/2017	SCR Upper
					Spawn	2/1/2020	ALP
Fall	982000362714306	106	14.1	23	Tag	10/14/2015	Sleepy Hollow
					Spawn	4/1/2018	Scar2
Fall	982000362714384	138	29.5	23	Tag	10/3/2017	121
					Spawn	1/27/2020	RSCDS, RSCUS
					Spawn	2/24/2020	SH2, SHUS
Fall	982000362714830	106	14	23	Tag	10/3/2017	121
					Smolt?	3/5/2018	RSC
					Smolt?	3/6/2018	CAWD1
					Smolt?	3/8/2018	RSC
					Spawn?	2/8/2020	RSCDS
Fall	982000362714960	162	53.9	23	Tag	9/14/2017	16
					Smolt	3/1/2018	RSC
					Spawn	3/16-4/9/2020	RSCDS, RSCUS
					Spawn	4/23-5/3/2020	SH2

Table 8 – continued from previous page

Event	PIT Tag	FL (mm)	Wt (g)	Tag Size (mm)	Category	Date	Site
					Kelt	5/16/2020	RSCDS
					Kelt	5/16/2020	RC
Fall	982000362714964	118	18.9	23	Tag	9/13/2017	Sleepy Hollow
					Spawn	3/2/2020	RSCDS, RSCUS
					Spawn	3/5-3/6/2020	SH2
					Kelt	4/1/2020	RSCUS, RSCDS
					Kelt	4/1/2020	RC
Fall	982000362724155	101	11.6	23	Tag	10/7/2016	Cachagua
					Spawn	1/25/2019	RSCUS
Fall	982000362724517	165	43	23	Tag	9/19/2016	Sleepy Hollow
					Spawn	3/19/2019	Scar2
					Spawn	3/22/2019	SH2
Fall	982000365197637	89	7.6	12	Tag	9/20/2017	Cachagua
					Smolt	4/21/2018	CAWD1, CAWD2
					Spawn	2/21-2/22/2020	RSCDS, RSCUS
Fall	982000365198458	89	7.2	12	Tag	9/27/2017	Compadres
					Spawn	3/30/2020	RSCDS, RSCUS
LP	982126053894565	99	10.1	12	Tag	4/26/2019	RST
					Spawn	3/17/2021	Weir
					Spawn	3/18/2021	RC
					Spawn	3/18/2021	RSCDS, RSCUS
					Spawn	4/9-4/12/2021	BLP

8 Tagged smolt and adult length comparisons

A key benefit to estimating smolting rate using PIT tags is that we can compare characteristics of the juveniles that emigrated with the juveniles that did not. This allows us to better understand the specific environmental conditions and restoration actions that promote smolt production. Fish size is one characteristic we thought would be important based on other studies.

We hypothesized that the larger tagged juveniles would be more likely to emigrate one year after tagging, and that the smaller tagged juveniles would be more likely to emigrate two years after tagging because marine survival is highly correlated with size (Ward et al. 2011). Additionally, tagged juveniles that returned to spawn two and three years after tagging would be the larger tagged juveniles because larger juveniles are more likely to survive their ocean migration. We expected that our hypothesis would apply equally to both fall-tagged juveniles, as well as the relocated-rescue summer-tagged juveniles.

For this initial analysis, we classified ‘year-one’ and ‘year-two’ emigrants based on detection patterns. If we observed a tagged juvenile downstream of its tagging site between January 1-May 31 one year after tagging, and we did not detect it again from June-December 31 that year, we classified it as a ‘year-one emigrant’, meaning it emigrated one year after tagging. Similarly, if we observed a tagged juvenile downstream of its tagging site between January 1-May 31 two years after tagging, and we did not detect it again from June-December 31 that year, we classified it as a ‘year-two emigrant’, meaning it emigrated two years after tagging. One concern about the year-two emigrant assignments was that it is possible that we missed the downstream migration in year two, so what we are calling a year-two emigrant is in fact a year-one emigrant and year-two spawner. We are working to improve the accuracy of these classifications for future analyses. ‘Year-two spawners’ are tagged juveniles that we detected as year-one emigrants the previous year, and were detected again the following year between January 1-May 31. ‘Year-three+ spawners’ are tagged juveniles we detected between January 1-May 31 three or more years after tagging.

To test our hypotheses, we compared the length frequencies (i.e., the number of juveniles at each FL) in each category against the overall length frequency of tagged juveniles from tag years 2017-2020. We converted the length frequencies to length density (i.e., the number of fish at each FL divided by the total number of fish) to standardize the values from 0-1 and to make the tagging and detection data visually comparable. We combined both tag sizes into this initial analysis because we were curious about the emigration and spawning patterns by length overall, and not tag size. However, this creates

an important consideration when interpreting the data because larger 23-mm tags have much higher detection rates than the smaller 12-mm tags.

Results of fall-tagged juveniles

Our hypotheses were not strongly supported in the fall-tagged juveniles. There was a higher density of year-one emigrants in the 100-200 mm FL size range and a lower density of fish <100 mm FL compared to the overall length densities of tagged fish (Figure 19, top panel). This suggests that there may be a slight propensity towards larger juveniles emigrating in the first year (or surviving to emigrate), however it is not an overwhelming pattern and could be attributed to the higher detection probability for juveniles >100 mm FL tagged with 23-mm PIT tags. A more definitive answer will require more sophisticated methods of analysis.

The year-two emigrant length densities were more consistent with our hypothesis in that a high density of juveniles <100 mm FL were detected emigrating two years after tagging. The fish that we classified as year-two spawners had a bimodal distribution that included an overabundance of small fish between 65-85 mm FL at the time of tagging and an overabundance of large fish in the 175-200 mm FL (Figure 19). This suggests that there may be many small fish migrating downstream into the lagoon at age 1, and returning to the river briefly before migrating to the ocean at age 2. This pattern has been observed in Scott Creek (Hayes et al. 2011) and represents a strategy by which individuals take advantage of the high growth potential in the lagoon.

Our hypothesis that there would be more large fish among the year 3+ spawners was supported by the data. Fish >100 mm FL had a much higher density among the year 3+ spawners than the fish originally tagged (Figure 19). This pattern could be due to several non-independent factors. Larger fish are more likely to survive between fall tagging and outmigration and they are more likely to survive in the ocean and return as spawners. Additionally, these larger fish are more likely to return three years after tagging, and given that we are only in our fourth year of the study, we would be more likely to detect these spawners compared with smaller fish more likely to return four or five years after tagging. Lastly, larger fish have larger tags, which have better detection at our antennas. All that to say, the year-3 fish do support the hypothesis that larger fish are more likely to survive and return to spawn, however this result should be revisited over the next few years to confirm.

Overall, we conclude that we need additional analyses to fully investigate the relationships between length at tagging, emigration, and smolting. There was not overwhelming evidence that larger fish in the fall would be more

likely to survive and emigrate in the subsequent spring, or return to spawn three or more years later. This suggests that small fish may have important contributions to the spawning run, and that lagoon rearing may also play a role by facilitating their rapid growth prior to ocean entry.

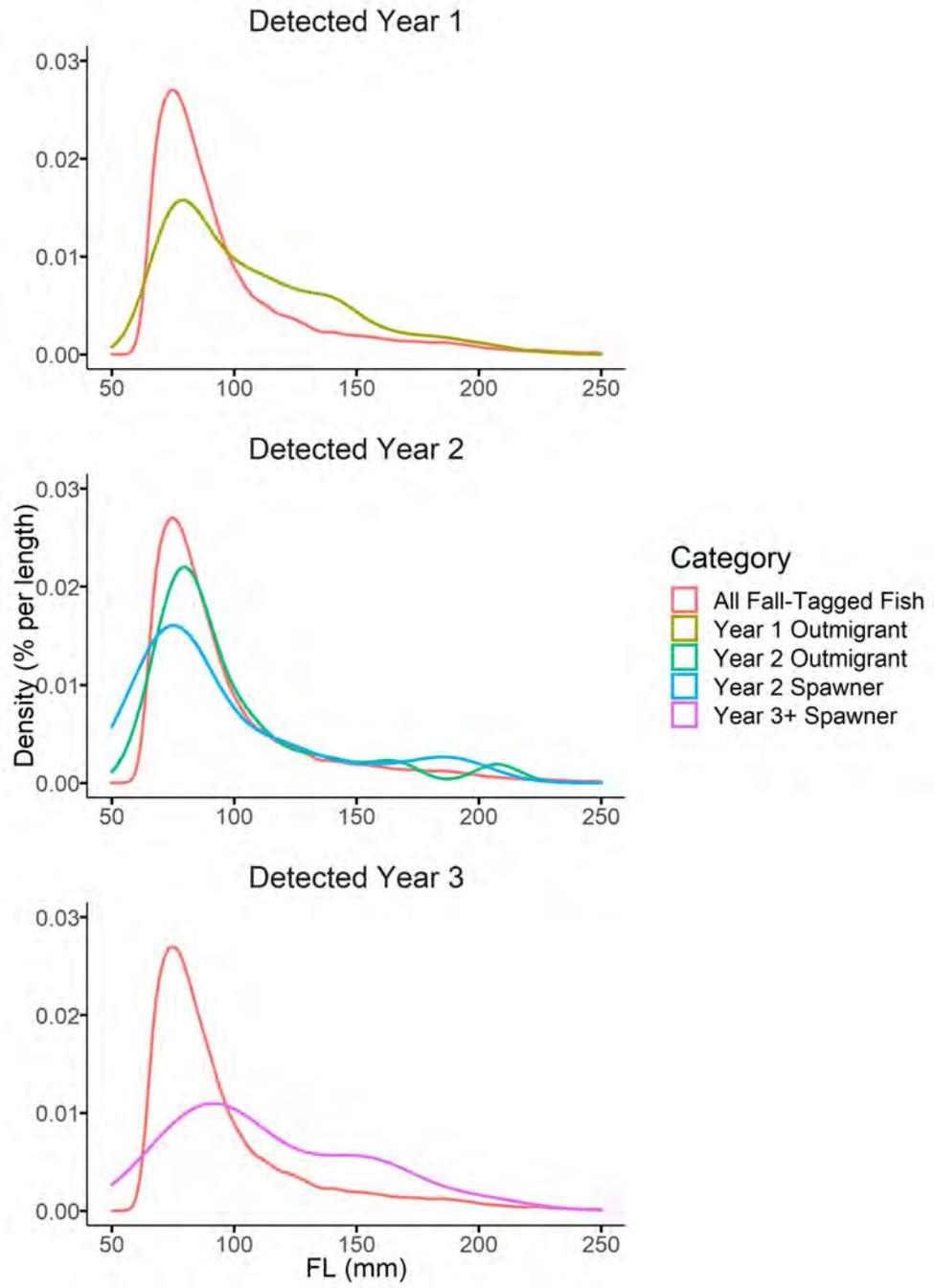


Figure 19: Length densities (standardized frequencies) of all juvenile fish tagged during fall population surveys between 2017-2020 compared with year-1 and year-2 outmigrants, and year-2 and year-3+ spawners.

Results of relocated-rescue summer-tagged juveniles

The length frequency patterns in the relocated-rescues largely vary based on where fish were rescued (Figure 20). Fish rescued in the lower Carmel River appear to have two age classes, we assume age 1 and age 2, and are larger than fish rescued in Cachagua Creek or the lower river tributaries that include Potrero, Hitchcock and Garzas Creeks (Figure 20). Therefore, when we compare size density by category with the initial size density, it is important remember that the larger tagged juveniles primarily come from the lower-mainstem Carmel River, whereas the smaller tagged juveniles primarily come from the tributaries.

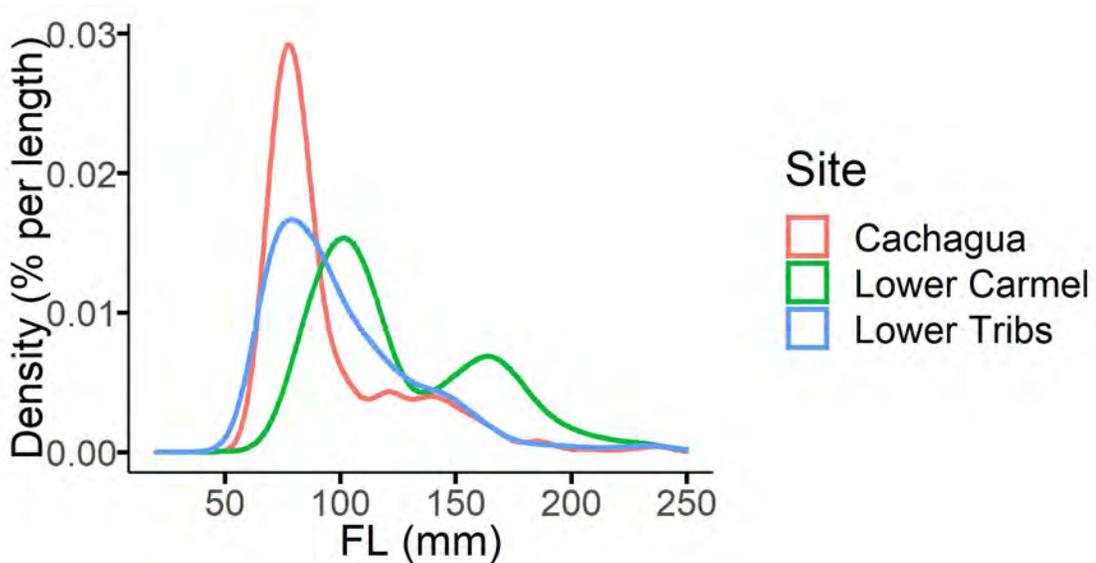


Figure 20: Length densities (standardized frequencies) of all juvenile fish tagged during summer rescue relocations between 2017-2020 divided by watershed region. The lower Carmel is the lower mainstem and the lower river tributaries include Potrero, Hitchcock and Garzas creeks.

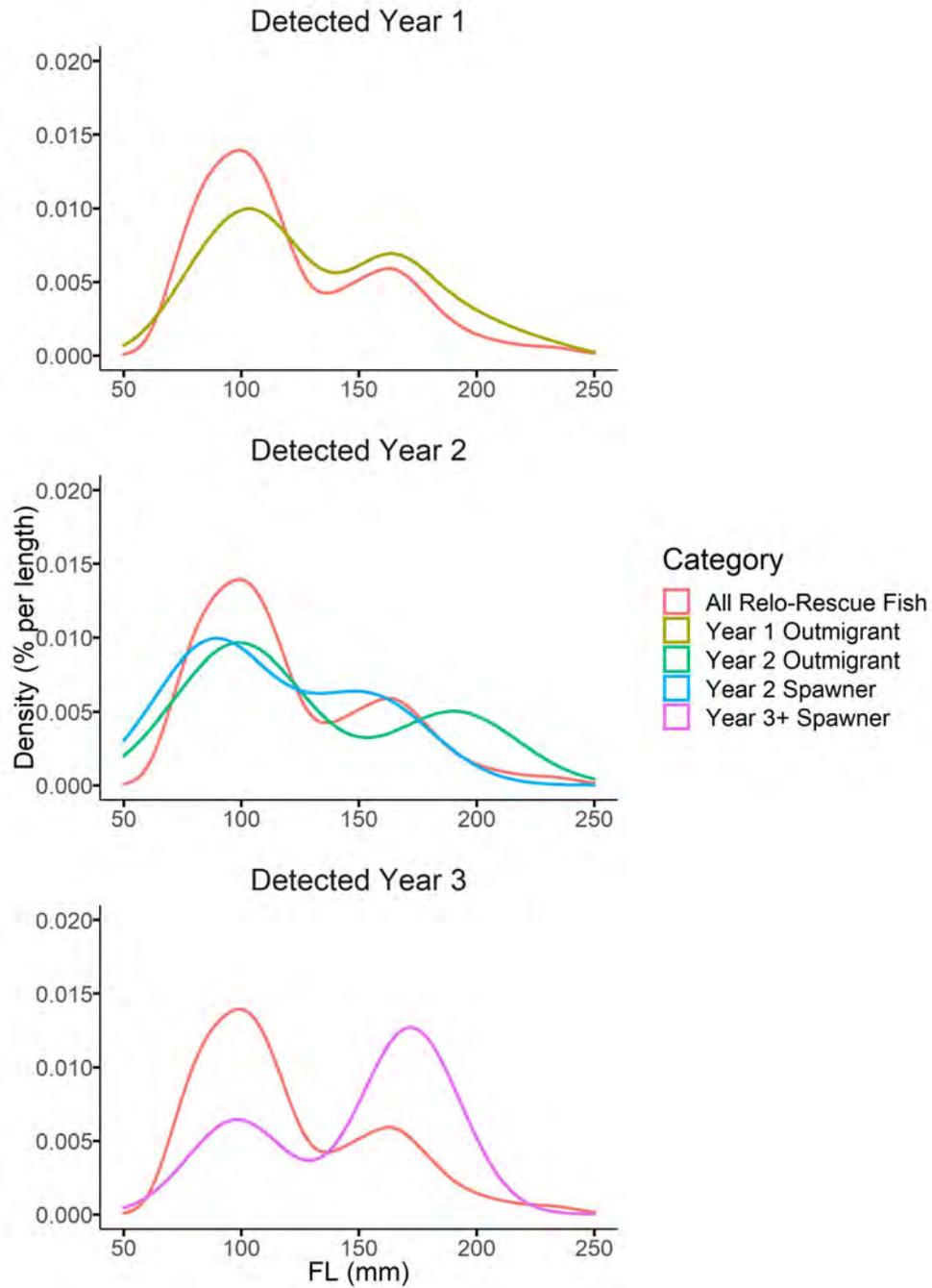


Figure 21: Length densities (standardized frequencies) of all juvenile fish tagged during summer rescue relocations between 2017-2020 compared with year-1 and year-2 outmigrants, and year-2 and year-3+ spawners. The majority of summer rescue relocations are from 2018.

The length pattern in the year-one rescue emigrants was similar to what we observed for the year-one fall emigrants. We observed that emigrants had a slightly higher density of large fish in the 120-250 mm FL size range and a lower density of fish <120 mm FL than the full set of fish we originally tagged (Figure 21). The fish that we classified as year-two emigrants had a bimodal distribution that included small (65-100 mm FL) and exceptionally large (150-250 mm FL) fish, whereas the fish we classified as year-two spawners had a higher density of all fish between 65-160 mm. This suggests that many of the smaller relocated rescues from the tributaries are migrating downstream into the lagoon at one year after tagging, and returning to the river briefly before migrating to the ocean in the second year, similar to our observations in the fall-tagged juveniles.

There was clear support for our hypothesis that larger tagged juveniles would be more likely to return as spawners three or more years after tagging. Fish >140 mm FL had a much higher density among the year 3+ spawners than the fish originally tagged (Figure 21). However, these spawners were made up of just six juveniles tagged in 2018, all of which were rescued and relocated from the lower mainstem (Table 8). This pattern should be interpreted with strong caveats related to the duration of our study and tag size, and should be revisited with data collected over the next few years. However, these initial data do suggest that larger relocated rescue fish are more likely to survive and return to spawn. While this length analysis needs further refinement, one major conclusion is that some of the rescued fish have been observed to survive to adulthood, and therefore contributed to the breeding population.

9 Carmel steelhead trends compared to other California populations

Our research over the past four years has focused on identifying factors and conditions that influence steelhead productivity in the Carmel River. As part of this research, we were curious if the steelhead trends we observe in the Carmel River are similar to those from other steelhead populations in California. If the trends in Carmel River steelhead are similar to other California populations, it suggests that regional drivers may have a strong influence and could mask the influences of local conditions, such as water withdrawals or restoration, and would provide an explanation for why the adult returns have declined in spite of extensive river restoration and fish rescues.

To compare Carmel steelhead productivity with other populations in California we searched for long-term steelhead return data. We limited our analysis

to populations with at least 16 years of data collected between 2001 and 2019 to ensure that we adequately captured populations dynamics. Nine populations met the criterion for 16 years of data (Table 9). Most of these populations are in relatively small coastal watersheds, although one is located in the Central Valley. All are winter-run steelhead (Figure 22).

We focused our analysis on two questions. 1. Do the nine populations have similar (shared) trends over time? 2. Are there regional drivers that can explain these trends?

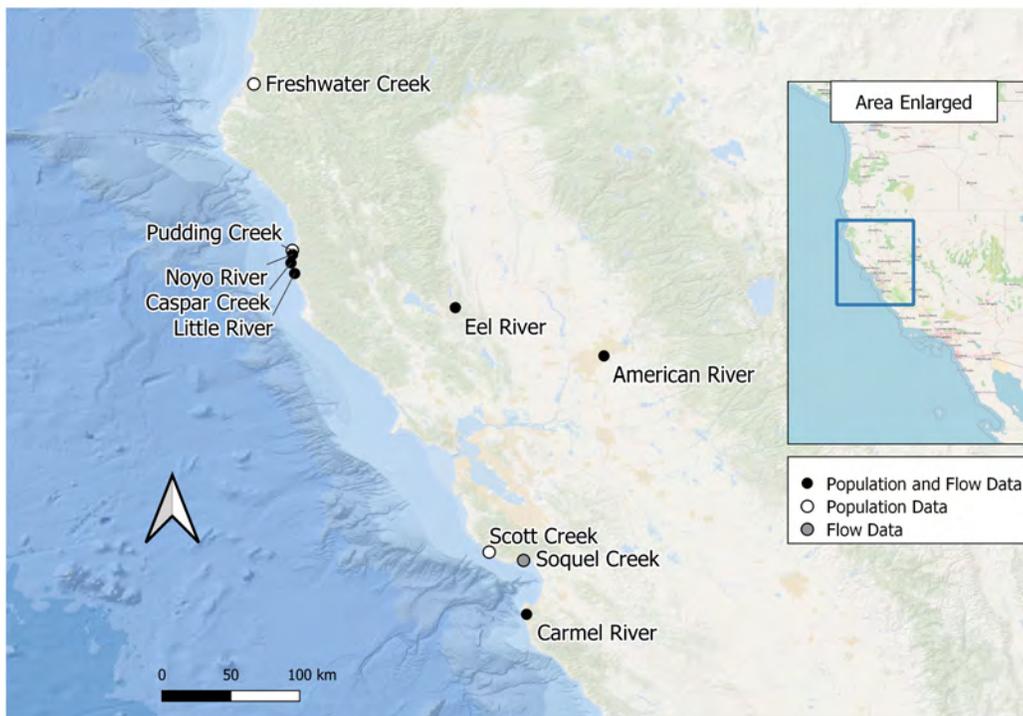


Figure 22: Locations of the nine steelhead populations and the paired stream-flow gages used in the analysis. All streamflow gages were operated by USGS, except for Caspar Creek which was operated by USFS.

Table 9: California steelhead populations used in the analysis.

Population	Lat. (°N)	Long. (°W)	Survey	Est. Method	Stream Gage	Air temp. Ecore- gion	Source
American River	38.61	-121.31	Redd Count	Expanded Redd Count	American (11446500)	TG	BoR
Carmel River	36.54	-121.93	Migrant Trap	Trap Count	Carmel (11143200)	TC	CalAm Water
Caspar Creek	39.36	-123.81	Spawning Ground	Mark- Recapture	N.F. Caspar (USFS)	TF	CDFW
Eel River	39.39	-123.12	Migrant Trap	Trap Count	Eel (11471500)	TF	CDFW
Freshwater Creek	40.8	-124.12	Weir	Mark- Recapture	Little River (11481200)	TF	CDFW
Little River	39.27	-123.79	Spawning Ground	Expanded Redd Count	North Fork Caspar (USFS)	TF	CDFW
Noyo River	39.43	-123.81	Spawning Ground	Expanded Redd Count	Noyo (11468500)	TF	CDFW
Pudding Creek	39.46	-123.81	Spawning Ground, Migrant Trap	Mark- Recapture2	North Fork Caspar (USFS)	TF	CDFW
Scott Creek	37.04	-122.23	Spawning Ground	Weir, Live- Fish	Soquel (11160000)	TF	National Marine Fisheries Service

Methods

To identify shared trends and identify regional environmental drivers, we used a method called dynamic factor analysis. Dynamic factor analysis fits the group of nine populations with a pre-specified number of shared trends (1 trend, 2 trends, etc.) that describe the way in which fluctuations of individual populations are shared across the entire set. We compare the models based on their fit to the data using an AICc score, which describes how well we expect the shared trends to generalize to additional populations or years of data. The model with the lowest AICc score is considered the top model and indicates the number of shared trends within the group of nine populations. In each model, a loading is calculated for each population that indicates how similar that population is to the overall shared trends. A loading of 1 would indicate a perfect fit between the shared trends and the individual population, and a loading of 0 would indicate no relationship between the shared trend and the individual population. The loadings also help us identify groupings within the nine populations. Detailed information on dynamic factor analysis is described in Zuur et al. 2003 and Holmes et al. 2020. In addition to identifying shared trends, we can use dynamic factor analysis to measure the relationship between regional environmental drivers, such as rainfall or ocean conditions, and the trends within the individual populations. For example, if the trends in six of the populations are similar to the pattern of regional rainfall over time, we infer that rainfall may be driving the trends we observe in those six populations.

Steelhead productivity

For the dynamic factor analysis, we converted the yearly return data (number of returning adult steelhead) to productivity estimates. Productivity estimates account for the number of parents that produce the run, and by making this conversion we are able to account for years that had a high number of parents vs. years that had a low number of parents. We searched the literature and found that California steelhead spawners are most commonly 3- and 4-years old, spending 1–3 years in freshwater and 1–2 years in the ocean (Busby et al. 1996; Dettman and Kelley 1986; Shapovalov and Taft 1954). Although there is some year-to-year variation, one to two age classes dominated in each year in the majority of populations. As a result of the literature search, we assumed that the adult age composition in a given year was half 3-year-olds and half 4-year-olds, and that the majority of individuals spent 1–3 years in freshwater and 1–2 years in the ocean in all of our study populations.

We calculated a return year productivity index based on the assumed age

structure to isolate the effects of environmental conditions from the possibility that a low (or high) number of spawners is simply due to a low (or high) number of parents. We transformed spawner abundances to return year productivity using the following equation:

$$y_t = \frac{n_t}{0.5(n_{t-3} + n_{t-4})}, \quad (4)$$

where y_t is the productivity index for adults returning to spawn in year t , n_t is the number of spawners returning in year t (i.e., the recruits), and n_{t-3} and n_{t-4} are the number of spawners returning in three and four years prior, respectively (i.e., the parents).

The assumed age structure was also important to how we handled the environmental data. Because the data we used is the number of returning spawners, we needed to infer what conditions they would have experienced in the past as freshwater juveniles, smolts, and during ocean residence.

Environmental Drivers

To identify the environmental conditions that may drive the observed trends in steelhead productivity, we conducted a literature search and identified 15 potential drivers. There are relatively few studies that have investigated the direct mechanisms between steelhead growth and survival, population dynamics, and environmental drivers. Therefore, the drivers that we identified are best characterized as hypothesized environmental drivers.

Freshwater Drivers There is compelling evidence that freshwater flow and temperature influence steelhead growth and survival at multiple points in their life cycle and in different seasons (Figure 23). Juvenile growth in coastal California streams is most limited seasonally during summer low-flow conditions (Harvey et al. 2006; Hayes et al. 2008; Sogard et al. 2009) and decreased juvenile survival is associated with lower summer flows (Grantham et al. 2012; Hwan et al. 2017). Juveniles migrate to the ocean (i.e., ‘outmigrants’) from February to May. Low flows and high temperatures during the outmigration season can directly impact downstream survival (Friedman et al. 2019), can increase predation at the river mouth (Osterback et al. 2014), can limit access to the ocean (Hayes et al. 2011), or have indirect nearshore mortality by limiting growth prior to ocean entry (Munsch et al. 2019). Returning adults may also be limited from ascending rivers by low flows and high temperatures when they migrate into rivers from December to March (Keefer et al. 2018).

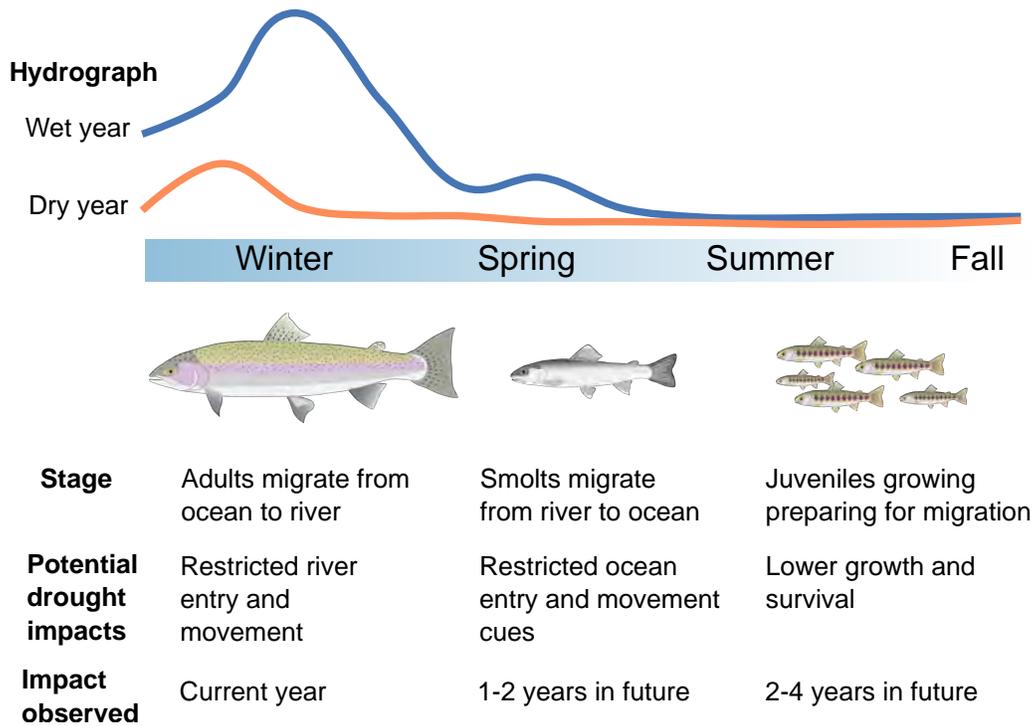


Figure 23: In Mediterranean climate streams, the rainfall during winter influences the flows for the rest of the year. Species with multiple stages and ages are each affected in different ways, resulting in population-level effects lasting multiple years. Steelhead adults returning to spawn during a winter drought will influence the population in that year. Steelhead smolts affected during their spring ocean migration will influence the number of returning spawners after spending one to two years in the ocean. Juvenile steelhead affected during summer drought conditions will influence the number of returning spawners after their freshwater and marine period ends, in two to four years.

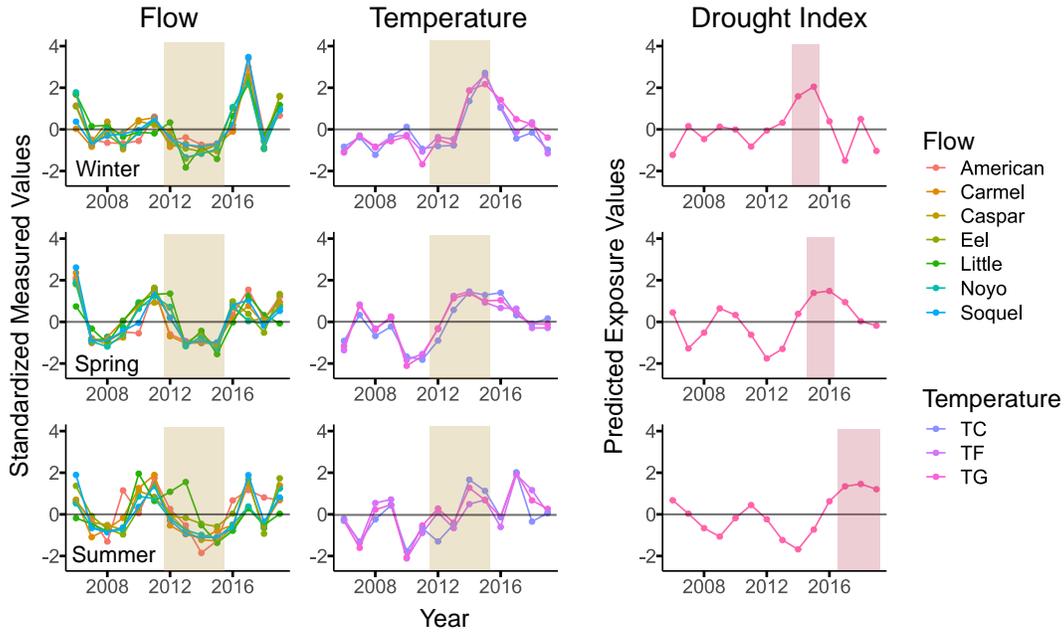


Figure 24: Standardized (z-scored) mean winter (Jan-March), spring (April-June), and summer (July-August) flow and temperature data. The streamflow data collected from nine stream gages in the study region showed strong covariance over the study period (2006-2019). The air temperature data collected from three ecoregions that cover the study region showed similarly strong covariance over the study period. The ecoregions were temperate conifer forests (TF), temperate grasslands, savannas and shrublands (TG), and Mediterranean forests, woodlands and scrub (TC). Streamflow and temperature data were transformed to estimate the exposure of each run year, and converted to a drought index by subtracting the transformed flow from the transformed temperature indices. The pink boxes indicate the run years that experienced above average drought conditions, and are therefore the years we expect to see below average steelhead productivity.

To characterize flow conditions, we utilized stream flow data from gage stations that were located in the same rivers as our population data, where possible, to compare flow conditions across the sample area and during summer, spring and winter (Figure 24, Table 9). Four rivers did not have gage stations (Freshwater Creek, Pudding Creek, Little River, and Scott Creek), so we used data from nearby streams of similar size. We estimated summer flow conditions as the mean of July, August, and September mean monthly flow, spring flows as the mean of March, April, and May mean monthly flow, and

winter flow conditions as the mean of December (of the year previous), January, February, and March mean monthly flow. Data from each gage in each season was standardized to a z-score (mean = 0, variance = 1), and plotted to compare the trends across rivers (Figure 24).

Temperature is also an important component of freshwater conditions, so we compared temperature across the study area during summer, spring, and winter. We used air temperature as a proxy for stream temperature (Mohseni and Stefan 1999) because existing stream temperature datasets were not geographically or temporally sufficient for our analysis. To calculate air temperature across the geographic extent of the populations, we filtered the PRISM Monthly Spatial Climate Dataset AN81m at 4 km resolution (Daly et al. 2008, 2015) by the three ecoregions that cover the geographic extent of the populations using Google Earth Engine (Gorelick et al. 2017). The ecoregions are defined by the RESOLVE Ecoregions dataset (Dinerstein et al. 2017) and the three ecoregions that covered the geographic extent of the populations were: Temperate conifer forests; temperate grasslands, savannas and shrublands, and; Mediterranean forests, woodlands and scrub. We estimated summer thermal conditions as the mean of July, August, and September mean temperature, spring thermal conditions as the mean of March, April, and May mean monthly temperature, and winter thermal conditions as the mean of December (of the year previous), January, February, and March mean monthly temperature. Data from each ecoregion in each season was standardized to a z-score (mean = 0, variance = 1), and plotted to compare the trends across ecoregions (Figure 24).

After confirming that seasonal flow and temperature had a consistent pattern between rivers and ecoregions, we averaged across the rivers and ecoregions to create regional, seasonal flow and temperature indices. Additionally, we calculated a drought index by combining regional, seasonal standardized flow and temperature indices into an overall drought score by adding the negative of the flow score to the air score. This assumes that high temperatures and low flows contribute equally to drought impacts, and that the magnitude of each is scaled relative to local historical variability (the z-score).

Marine Drivers There is also compelling evidence that marine conditions influence steelhead growth and survival during their marine juvenile phase. We identified an additional six potential marine drivers through our literature search: three nearshore drivers and three offshore drivers. We decided not to include Pacific Decadal Oscillation (PDO) or North Pacific Gyre Oscillation (NPGO) even though these have been identified as significant drivers in other

studies (e.g., Courter et al. 2019). The reason is that PDO and NPGO are broad-scale climate drivers that effect a large suite of marine and terrestrial conditions simultaneously, while our focus was on drivers as particular points of impact on the steelhead life cycle. Unlike with freshwater conditions, we assumed the spatial exposures were the same for all nine populations.

Nearshore Drivers Steelhead smolts are unique among other species of Pacific salmon in that they tend to enter the ocean at a larger size, typically 14–20 cm FL (Quinn 2005; Wagner et al. 1963), and move quickly north along the coastal shelf until they reach Vancouver Island, where they travel west to offshore feeding grounds in the Gulf of Alaska by early summer (late June–early July; Brodeur et al. 2004; Daly et al. 2014). Despite their relatively larger size and rapid transit through the coastal waters, the early marine life stage is thought to be a critical period for growth and survival, influenced by nearshore ocean conditions (Friedland et al. 2014). The nearshore ocean conditions for our nine populations are structured by the California current and associated coastal upwelling that controls both temperature and food availability (Santora et al. 2012). Below we develop three indices to characterize thermal exposure and food availability during nearshore ocean transit.

Habitat Compression Index To estimate the amount of cool upwelling habitat available to smolts entering the ocean, we utilized the habitat compression index developed by Santora et al. (2020). The habitat compression index estimates the amount of cool water ($<12^{\circ}\text{C}$) at 2 m depth adjacent to the coastline from 35.5–40°N. We averaged March, April, May habitat compression indices to estimate an annual amount of smolt season upwelling habitat. We predicted that years with less cool water area (i.e., a lower habitat compression index) would be associated with lower steelhead productivity.

Rockfish and Krill Nearshore feeding opportunities should be a key influence on growth and survival after the vulnerable transition from rivers to the ocean. Steelhead smolts primarily feed on small fish and zooplankton, including krill and YOY rockfish (Daly et al. 2014; Thalmann et al. 2020). Catch-per-unit-effort of coastal shelf krill and YOY rockfish are collected by NOAA-NMFS during May–June annually (Sakuma et al. 2015). The survey spans most of the California coast from Monterey Bay to Point Reyes (36–3°N). We predicted that years with high YOY rockfish or shelf krill abundances would be associated with greater steelhead productivity.

Offshore Drivers After leaving the coastal shelf, steelhead distribute widely across a northerly band of the Pacific Ocean, extending across the entire sub-arctic North Pacific from the North American coastline to southern Kuril Islands, Russia, and from 40°N to 52°N in the Gulf of Alaska and south of 48°N in the central North Pacific (Myers 2018 and references therein). Sea temperatures, food availability, and abundance of competitors are the most likely factors influencing steelhead distribution, growth and survival in the high seas (Pearcy et al. 1988; Weitkamp and Sturdevant 2008), although the difficulty in capturing steelhead and their prey in the high seas prevents us from fully understanding these relationships (Myers 2018).

Thermal marine habitat Sea temperature appears to be a primary physical factor influencing the distribution of steelhead in the open ocean, and a primary factor in their growth and survival (Atcheson et al. 2012*a,b*; Kaeriyama et al. 2004). Steelhead are almost always found between the 15°C and 5°C sea-surface temperature isotherm, and shifts in distribution are associated with seasonal changes in sea surface temperature (Burgner and Commission 1992; Pearcy and Fisher 1990; Sutherland 1973).

We estimated the amount of ‘thermal marine habitat’ as the number of square kilometers within the historic range of steelhead that experienced 5–15°C temperature during June, July and August. We mapped a polygon encompassing the known steelhead ocean distribution (Burgner and Commission 1992; Myers 2018; Welch et al. 2000) with the following perimeter coordinates: ([160°E, 52°N]; [150, 42]; [200, 42]; [200, 44]; [235, 44]; [225, 60]; [205, 60]; [203, 57]; [200, 56]; [190, 52]; [160, 52]), and then clipped the polygon to exclude areas less than 1 km from shore. We then calculated the mean number of square kilometers within this polygon that were between 5–15°C for June through August of each year using sea surface temperature data from the NOAA 1/4 degree daily Optimum Interpolation Sea Surface Temperature dataset (Reynolds et al. 2008). The mapping and analysis were done in Google Earth Engine (Gorelick et al. 2017). We predicted that lower thermal marine habitat would be correlated with decreased steelhead productivity.

Pink Salmon abundances Steelhead diet quality (high proportions of squid and high prey density) has been negatively correlated with abundances of eastern Kamchatka pink salmon (*O. gorbuscha*) in the Central North Pacific, suggesting pink salmon may compete with steelhead and negatively influence their diet (Atcheson et al. 2012*a*). We used total annual pink salmon abundance data (wild plus hatchery) as an index of competition effects on steelhead.

Data for 2001 to 2016 was from Ruggerone and Irvine (2018), and data from 2016–2018 was compiled separately using the same methods (Ruggerone 2020). We aggregated the regional pink salmon data into two large regions of Asia and North America. Asian populations included Japan, Russian mainland and islands, Eastern Kamchatka, and Western Kamchatka. North American populations included Alaska Southern Peninsula, Kodiak, Cook Inlet, Prince William Sound, Southeast Alaska, Northern and Southern British Columbia, and Washington. We predicted that exposure of steelhead to high abundances of pink salmon in either region would predict low steelhead productivity.

Results

We first fit three models without environmental drivers to determine the overall number of trends. The three models were 1-, 2-, and 3-trend models. The model with the best fit (lowest AICc score) was a single trend model. The AICc scores were 320, 325, and 333 for the 1-, 2-, and 3-trend models, respectively. The loadings were greater than 0.4 for seven of the nine populations (Figure 25). The seven populations included Freshwater Creek, Pudding Creek, Caspar Creek, American River, Little River, Scott Creek, and Carmel River. The Carmel River had a loading of 0.58, which suggests that its trend is very similar to the trend shared among the seven populations.

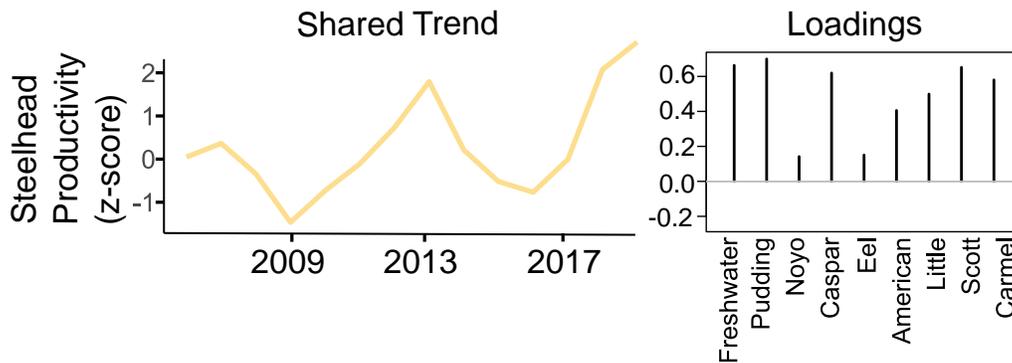


Figure 25: The shared trend in steelhead productivity fit by the DFA, and the similarity (i.e., loading) of each population to that shared trend.

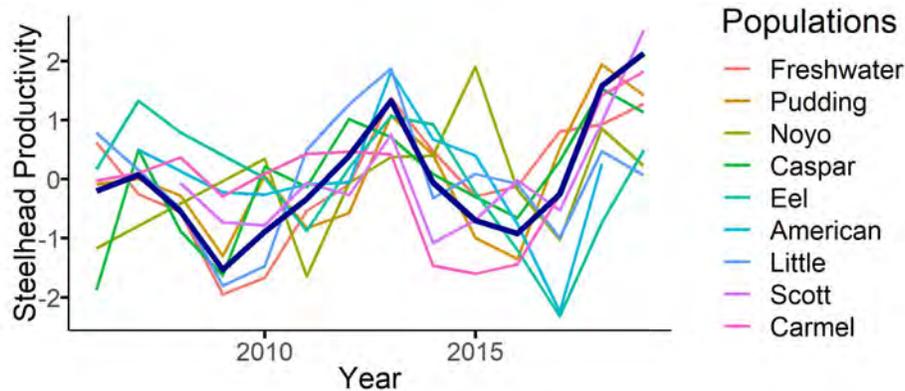


Figure 26: Steelhead productivity of each population by return year plotted with the shared trend fit by the DFA (dark blue line).

The shared hidden trend was below average for most of 2006 to 2012, well before the predicted drought impacts in 2014 (Figures 25, 26). Productivity dipped again in 2014 to 2016, concordant with drought impacts on adult spawners and spring outmigrants, but then reached peak values from 2017 to 2019, immediately after the end of the drought and too soon to be consistent with drought impacts on juvenile rearing. The well below average productivity in 2017 in the Eel and American Rivers suggests a greater drought impact on spring outmigrants and/or summer juvenile rearing. However, the increased productivity in 2018 and 2019 in both of those populations indicates that the drought impact on juvenile rearing was not consistent for the duration of the drought.

After identifying the 1-trend model as the top base model, we fit 15 separate one-trend, equal variance models each with a single environmental driver. Seven of the drivers matched our a-priori predictions about the sign of the effect (positive or negative), while eight did not or were not consistent (Figure 27). Most driver effects were not significantly different than zero (i.e., the 95% confidence interval included zero) for the majority of populations. The three drivers that had significant effects in a majority of populations and matched our a-priori predictions about the effect sign were flow, temperature, and drought exposure indices during the outmigration stage (Figure 27). Additionally, the two drivers that consistently matched our a-priori predictions about the effect sign, but were not statistically different from zero, were thermal marine habitat and North American pink salmon.

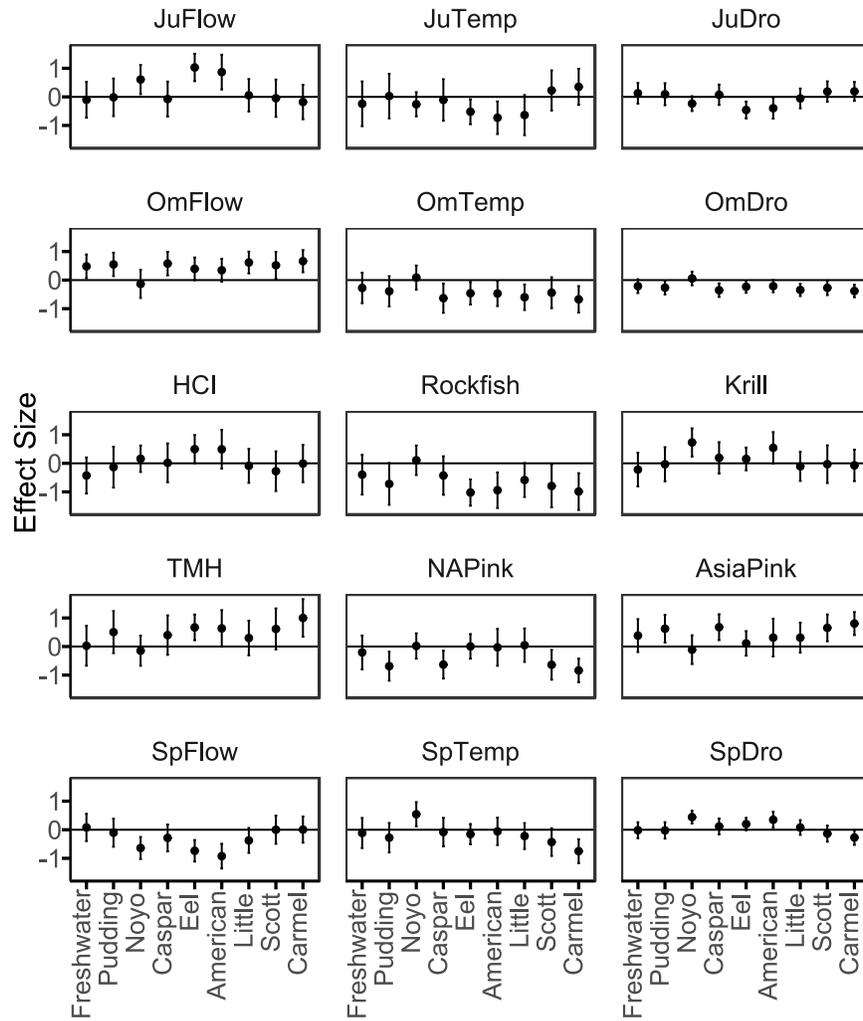


Figure 27: Effect sizes and 95% confidence intervals of the fifteen environmental drivers included in the null model (one-trend, equal variance) separately. All environmental drivers were standardized (z-score) prior to inclusion in the model, so their effect sizes are comparable.

Outmigrant condition indices had the most consistent and significant effect sizes, and supported the hypothesis that lower spring flows were associated with lower steelhead productivity (Figure 27). If we had only done this analysis in the Carmel River, we would have interpreted this result to mean that low flows limit the outmigration of smolts into the ocean, and fewer smolts entering

the ocean leads to fewer adult returns 1-2 years later. However, the Carmel River is the only river in which smolt ocean access is consistently limited by low flows. The other eight rivers retain smolt access to the ocean in most years. Therefore, effect of outmigrant conditions is not the result of access. We hypothesize that the effect is instead related to growth. Juvenile steelhead rely on feeding territories, and less water means less feeding habitat overall (Grant and Kramer 1990). Juvenile steelhead have the highest growth rates during winter and spring (Hayes et al. 2008; Figure 28), and because larger smolts have higher survival (Bond et al. 2008), the winter and spring growth surge may have significant impacts on overall smolt survival.

It was notable that juvenile (summer) flow conditions were significant in only three populations (the American, Eel, and Noyo rivers). The remaining populations had small and inconsistent effects (e.g., less than ± 0.18). This was a surprise because we generally think of the summer low flows as the most limiting. However, this result suggests that may not be the case. These findings require further study.

While not statistically significant, thermal marine habitat effects were notable because many of the point estimates were large (Figure 27). All but three populations had point estimates greater than 0.4. However, the confidence intervals were also quite large, so only two populations were significantly different than zero. The large point estimates suggest that warm ocean conditions (i.e., low thermal marine habitat) harm steelhead productivity. Thermal marine habitat was strongly negatively correlated with outmigrant temperature (-0.71) and drought (-0.56) indices, leading us to conclude that both thermal marine habitat and outmigrant freshwater indices are plausible drivers.

Pink salmon was a significant effect for four populations (Carmel, Caspar, Pudding, and Scott); however, the signs were opposite for Asian and North American pink salmon (Figure 27). Our a-priori prediction was that high pink salmon abundance would cause lower steelhead productivity because of competition for food. North American pink salmon were negatively correlated with steelhead abundance, as predicted, but Asian pink salmon were positively correlated, which could indicate the opposite relationship wherein both steelhead and pink salmon productivity is controlled by a similar mechanism. Asian and North American pink salmon are strongly negatively correlated at -0.815, so an effect observed in one would be have the opposite effect in the other. Additionally, Asian Pink Salmon were negatively correlated with smolt temperature and drought indices (-0.58 and -0.6, respectively), so the positive Asian Pink Salmon effect could also be due to the relationship between productivity and outmigrant conditions.

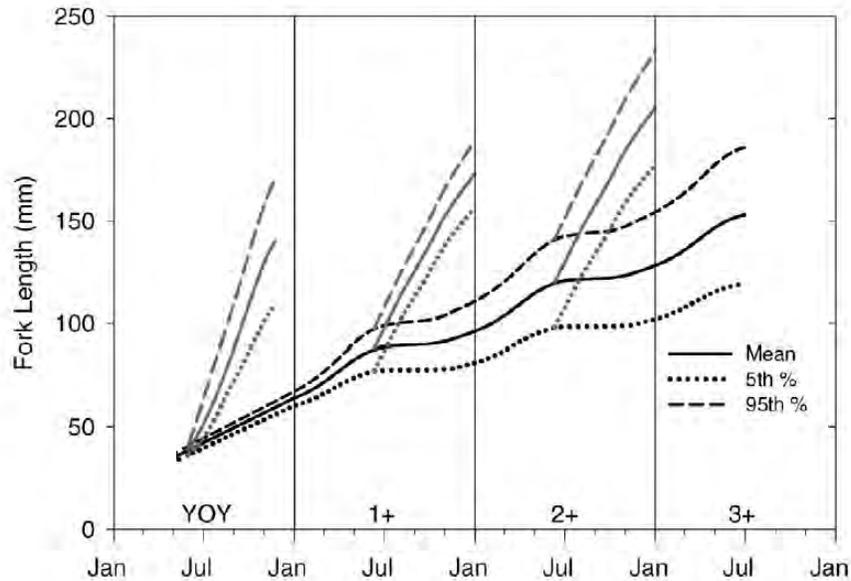


Figure 28: Figure adapted from Hayes et al. 2008 showing growth trajectories of juvenile *O. mykiss* in the Scott Creek watershed. The growth trajectories are based on changes in fork length observed in resampled age-0 fish during the first 8-10 months after emergence and larger PIT tagged individuals (ages 1-3 and older) that were recaptured in the upper watershed (black lines) or estuary (gray lines).

Conclusions

Our overall conclusion is that steelhead productivity in the Carmel River is not unique among California steelhead. Since 2001, Carmel steelhead productivity has followed a trend similar to other coastal California populations. The trend shared among six of the nine populations can be partially explained by outmigrant flow, outmigrant temperature, and outmigrant drought exposure indices, as well as thermal marine habitat and North American Pink Salmon abundances. These correlations suggest that these environmental drivers may be responsible for the steelhead productivity trends we observe, and those relationships are shared among many California populations. By accounting for the important regional drivers, we will be able to better understand the relationships between local conditions and actions and steelhead productivity in the Carmel River. The outmigrant flow and temperature are amenable to management strategies to improve smolt production and thus adult returns in

the Carmel River, and support our assumption of our tagging work that we need to better understand limiting factors between the end of the dry season and smolt migration the following spring. However, thermal marine habitat and Pink Salmon exposure are not amenable to management strategies within the Carmel and may represent a fundamental limit on scope for improvement. Lastly, the relationship between outmigrant flow, outmigrant temperature, and outmigrant drought indices deserves further study and is particularly relevant to discussions about water management in the Carmel River.

10 Population Status

After summarizing the research activities of the past several years, it seems reasonable to ask: are we any closer to explaining the lack of recovery in Carmel River steelhead? We believe we are. Here is what we know.

When we look at the Carmel steelhead runs in the context of how other nearby populations are doing, we see that most populations (including Carmel) have followed a similar trend over the past 20 years, and that trend is largely associated with a combination of spring flow conditions, pink salmon abundances in the north Pacific Ocean, and/or summer ocean temperatures in the north Pacific Ocean. Recent drought and warm ocean conditions have apparently resulted in very poor conditions for steelhead, and the low steelhead returns in the Carmel River over the past eight years can be partially attributed to these regional conditions.

With that said, we have also observed that local conditions influence steelhead production. There has been a strong relationship between low summer stream flows and low juvenile abundances (per spawner) since 1991. Our analysis suggests that low summer flows in the Lower Valley have decreased juvenile densities there relative to the Upper Valley and Canyon, and blocked juveniles from entering and using the lagoon during summer. Both of these impacts have likely hampered steelhead recovery. In addition, smolt production was low in 2017-2019 (emigration rates $\leq 15\%$). We are only beginning to identify what local environmental conditions may be related to smolt production, but the low values suggest local limitations and room for improvement.

Although the lagoon was never a specific focus of our research, it showed up as an important component in several of our analyses. Juvenile densities were lower when the river was connected to the lagoon during summer, suggesting that juveniles may be moving downstream to use the lagoon for summer rearing and growth. We directly observed some juveniles rearing in the lagoon during summer, and some of those individuals molting the following spring, and one

returning to spawn. Relocated rescues were observed moving downstream in the early winter before the lagoon was connected to the ocean, suggesting that those subdominant individuals may be using the lagoon for a burst of growth prior to smolting. How and when steelhead use the lagoon, as well as the impacts of the continued summer river-lagoon disconnect, are topics that should be studied further because they may be an important component to steelhead recovery.

The two mitigation measures that we examined, the change in summer pumping locations and relocation rescues, both appear to have produced detectable benefits for the population. The pumping strategy of California American Water has generally been effective at maintaining surface flow in the Upper Valley and the juvenile abundances there are 4.5 times higher than in the Lower Valley, where flows are much lower. In that way, this mitigation measure has been a success for the population. At the same time, this analysis shows that dewatering the Lower Valley has the combined negative effect of decreasing juvenile steelhead production in that strata, as well as blocking juvenile passage to the lagoon for summer rearing, which may be an even more important component of juvenile (and smolt) production than in-river rearing habitat.

The relocation rescues have also been effective at taking fish that would have otherwise perished and getting them to the smolt and spawner stages. The stock-recruit analysis suggested that on average, about 10% of relocated fish survived to the end of the dry season, whereas without rescues likely none of them would have survived. Our PIT tag data shows that some relocated rescues have smolted and some have returned as spawners, both of which contributes to the population overall. At the same time, relocated-rescued juveniles are not behaving in the same way as fall-tagged juveniles, especially with regards to spring outmigration. Relocated-rescued juveniles moved downstream from November-January, whereas fall-tagged juveniles moved downstream from March-May. The early outmigration movement could be due to the subdominant status of relocated-rescued juveniles or their inability to find quality habitat after being relocated. The different movement timing may mean that relocated rescue actions are most successful in years when the river is connected to the lagoon early in the season. Additionally, we still do not know if relocation rescues have unintended negative consequences, such as increasing density-dependent mortality or decreasing growth.

11 Adaptive Management

We are recommending three adaptive management actions based on the results of the studies described in this report. Our first recommendation is to try relocating summer-rescued juveniles to the lagoon instead of the river, and test the effectiveness of this strategy with PIT tags. In a Mediterranean river system where the lagoon stayed connected to the river year-round, we would expect to see subdominant or excess juveniles migrate downstream from the river to the lagoon during spring and summer. Subdominant juveniles are those without a quality territory and ‘excess’ juveniles are those in excess of the instream carrying capacity. These juveniles would rear in the lagoon until the following winter or spring, then migrate to the ocean as smolts.

We hypothesize that the current strategy of rescuing and relocating upstream has two effects on the juveniles: it takes away individual territories, which makes the individuals subdominant, and it increases upstream numbers (10% of fall fish were relocated-rescued juveniles; Chapter 3), which could push in-stream habitat over carrying capacity and entice juveniles to emigrate naturally. The relocated-rescued juveniles we monitored with PIT tags exhibited behaviors of subdominant or excess juveniles – they moved a lot in July when fall-tagged juveniles did not, and they moved downstream (possibly to the lagoon) as soon as the river reconnected to the lagoon in November, whereas the fall-tagged juveniles waited until March to move downstream (Chapter 6). Relocating rescues to the lagoon more mimics what would happen to subdominant or excess juveniles naturally. This is supported by our observation that when the river and lagoon stayed connected during high water years, we observed fewer juveniles in the fall, and we think this could be due to juvenile emigration from the river into the lagoon (Chapter 3).

We recognize that relocation rescues only occur when the Sleepy Hollow Rearing Facility is not operational or is over capacity, however this happens often enough that it is worth considering the lagoon as an alternative placement location to the river. We strongly recommend setting up an experiment that would relocate half of the rescues to the river, half to the lagoon, and tag all with PIT tags to compare the relative survival, smolting rates, and adult return rates. Depositing the rescues in the lagoon instead of the river is a relatively simple management change that could make rescue relocations much more effective and improve steelhead returns. However, the success of this management change is likely contingent upon the extent of striped bass (*Morone saxatilis*) predation and poor water quality, which brings us to our second recommendation.

Our second recommendation is to study the impact of striped bass on

juvenile steelhead rearing or passing through the lagoon. Striped bass are known steelhead predators that have been observed in the Carmel lagoon since at least the 1980's, and anecdotal observations suggest their numbers have increased in recent years. Both the California Department of Fish and Wildlife and the Carmel River Steelhead Association have collected separate lines of evidence that striped bass are consuming steelhead, though the quantity and impact on the steelhead population remains unclear. The juvenile steelhead we tagged in the lagoon in 2019 had a minimum survival rate of approximately 10% from June to November, followed by relatively high smolting rates and marine survival (Chapter 6). These results indicate that even with striped bass predation, some lagoon-rearing juveniles survive and contribute to the adult returns. Quantifying the steelhead consumption by striped bass, as well as the overall impact on the steelhead population, would help provide a blueprint for management actions such as releasing rescues into the lagoon and the on-going discussions about lagoon and floodplain restoration.

Our third, and final, management recommendation is to study the mechanistic relationship between spring flows and steelhead returns in the Carmel River, and consider water management strategies to increase spring flows or extend the spring flow period when the river is connected to the lagoon. Spring flows were highly correlated with adult returns in the Carmel and other central-coastal populations (Chapter 9), however the mechanism driving that relationship is unknown. One possibility is that years with increased spring flows provided better growing conditions that led to larger, and better surviving smolts. Winter and spring are the peak growing periods for in-stream juveniles (Hayes et al. 2011; Figure 28), and increased flows could provide more habitat and better growing conditions that lead to larger and better surviving smolts. Another possibility is that years with increased spring flows had a longer duration of connection between the river, lagoon, and ocean, so more fish had an opportunity to smolt or enter the lagoon. Understanding the mechanism that drives the relationship between spring flows and adult returns would identify what aspect of the spring flows is important (i.e., amount of water or duration), and could lead to specific water management objectives.

Lastly, we want to emphasize the utility of the adult weir that was installed by MPWMD in the lower river in 2021. Fish capture and monitoring at this weir will provide critical data on the number of adults returning to the Carmel River, as well as the timing, ages, and size structure of the adults. This data will be key for a future life-cycle model and general management of the Carmel River steelhead.

12 Acknowledgments

These projects would not have been possible without the input, guidance, and field efforts of Cory Hamilton at MPWMD. His contributions have improved many aspects of these projects. Beverley Cheney, Kevan Urquhart, and Thomas Christensen (each with MPWMD) have also contributed to these projects. The fieldwork was conducted by Tim Kahles, Brennan Helwig, Jordan Besson, Matt Johnson, Trevor Masters, Megan Pentecost, Tim Paulson, Issac Rodriguez, Julia Karo, Marina Lesse, Robert Manos, Ricky Marvin, Jonathan Stewart, Emerentia Kruse, Marina Hernandez, Dan Atkins, Eric Lumas, Jeff Harding, Ken Johnson, and Cole Neal. Gabriel Brooks (NOAA NWFSC), Gus Wathen (ELR), and Vince Tranquilli (ODFW) contributed to antenna design, installation, and troubleshooting. Aman Gonzalez, Chris Rudolf, Robert Coppola, Tony Lapham, and the greater Cal Am team at Los Padres have been supportive of the project and for that we are grateful. Nate Mantua and Dave Rundio (each with NOAA SWFSC) provided logistical support and study design input. Brian LeNeve and the CRSA members provided important local knowledge that informed our research. Bruce Dormody graciously provided access to his property for fall sampling, and provided his knowledge about flow conditions.

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