California Fish and Game 98(4):185-201; 2012

Identifying factors limiting coho salmon to inform stream restoration in coastal Northern California

SEAN P. GALLAGHER*, SHAUN THOMPSON, AND DAVID W. WRIGHT

California Department of Fish and Game, 32330 North Harbor Drive, Fort Bragg, CA 95437, USA (SPG, ST)

Campbell Timberlands Management, LLC, PO Box 1228, Fort Bragg, CA 95437, USA (DWW)

*Correspondent: sgallagh@dfg.ca.gov

We evaluated an eleven-year (2000 to 2011) coho salmon adult, parr, and smolt abundance data stream from three census watersheds in coastal Mendocino County, California to determine how this information can provide a scientific basis for directing life-stage specific stream restoration activities. The three census watersheds: Caspar Creek, Pudding Creek, and the South Fork Noyo River called Life Cycle Monitoring Streams (LCMS), are part of the California Coastal Salmonid Monitoring Plan. These LCMS are places where we estimate adult, parr, and smolt abundance; make connections between life stage abundance and abiotic factors; and serve as focal points to foster additional watershed and salmon research. Adult and smolt abundance was estimated using capture-recapture methods where fish were marked with either batch marks or individual identifiers and we estimated parr abundance with depletion sampling. Since 2006, we have applied Passive Integrated Transponder (PIT) tags to parr and smolts >70 mm and used this information to estimate abundance and survival. We used these data to calculate marine and freshwater survival, estimate carrying capacity of the three streams, and investigate the relationship between survival and abiotic factors (stream flow, turbidity, and temperature). We present the findings of this analysis and our results in relation to habitat census evaluations conducted during summer 2011. Finally, we discuss the application of our findings to restoration using large wood, and provide recommendations for future work to increase coho salmon production.

Key words: California, coho salmon, habitat, Mendocino County, Oncorhynchus kisutch, Oncorhynchus mykiss, Oncorhynchus tshawytscha, restoration, survival In coastal California, Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), and steelhead (*O. mykiss*) are listed under the California and federal endangered species acts. These listings require monitoring to provide measures of recovery (Good et al. 2005). The listing of these, and many other Pacific salmon populations, has led to extensive recovery efforts (Roni et al. 2010). The recovery plans for California's coastal coho salmon (National Oceanic and Atmospheric Administration [NOAA] 2010, 2012) require monitoring of population responses to recovery actions. The state of California's Fisheries Restoration Grant Program (FRGP) has expended \$180 million since 1981 on restoration of anadromous fish habitat. Bernhardt et al. (2005) estimated that over a billion dollars has been spent on watershed restoration in the Pacific Northwest since 1991. Nevertheless, Roni et al. (2010) reported that much uncertainty remains over the effectiveness of various restoration techniques. Indeed, studies linking habitat improvements with increased fish abundance are rare (Roni et al. 2008).

There is increasing evidence that a lack of winter habitat (slow water pools with cover for small fish) limits coho salmon production in coastal streams (Nickelson et al. 1992). Solazi et al. (2000) increased coho parr and smolt abundance and over-winter survival by creating and enhancing complex habitat using "large wood" (channel spanning logs). Similarly, Johnson et al. (2005) found that addition of large wood significantly increased coho salmon freshwater survival. Both of these studies required many years of pre-treatment and post-treatment monitoring, and treatment of large portions of their study streams. Roni et al. (2010) reported that considerable restoration is necessary to produce measurable changes in fish abundance. They suggested that flood plain and instream habitat restoration of 80% (reconnecting the flood plain and addition of wood to 80% of the stream) is required to double coho salmon smolt production; restoring 20% of the stream resulted in an increase of 25%. Focusing on particular habitats that limit salmon production and implementing restoration efforts lower in the river system should be even more efficient (Roni et al. 2010). In addition, protecting high quality habitats, restoring stream connectivity (Roni et al. 2008), and linking restoration sites to ephemeral streams and springs (Roni et al. 2010) should further increase the likelihood that restoration will result in more smolts. To our knowledge, the links between coho salmon production and their habitats has not been thoroughly investigated in coastal California.

The California Department of Fish and Game (CDFG) and Campbell Timberlands Management, LLC (CTM) have been conducting coho salmon and steelhead life cycle monitoring in three streams in coastal Mendocino County since 2000. Annual smolt-trapping and parr-rearing data collection began in mid-1980 in a few streams in coastal Mendocino County (S. Harris, CDFG, personal communication, March 2012). With funding from the FRGP and technical oversight from NOAA, CDFG and CTM began intensive life cycle monitoring in Caspar and Pudding creeks and the South Fork Noyo River in winter 2005 (Figure 1). Combining these data with our earlier work provided an 11-year time series (2000 to 2011) on abundance of adult, parr, and smolt coho salmon. If further grant funding becomes available, we expect life cycle monitoring to continue in these streams for many years, especially given the importance of these data to the California Coastal Salmon Population Monitoring Plan (CMP; Adams et al. 2011).

An important aspect of salmon life cycle monitoring is an understanding of the relationships between habitat and salmonid survival (Adams et al. 2011) to help interpret regional trends and direct effective restoration actions (NOAA 2010, 2012). We examined our 11-year data set (Figure 2) to evaluate (1) the relative importance of survival at different

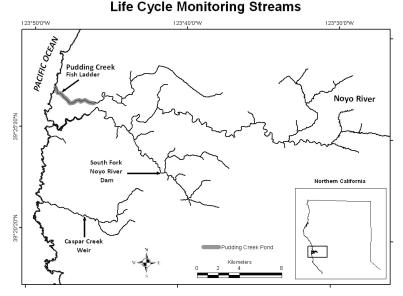


FIGURE 1.— Location of coho salmon life cycle monitoring streams in coastal Mendocino County, California.

life stages; (2) potential density dependence within life stages; (3) relationships between life stage specific survival and readily available physical stream factors (flow, temperature, and turbidity); and (4) carrying capacity among streams. We hypothesized that density dependence occurs in freshwater life stages and that some seasonal physical factors limit salmon populations. To help interpret the results of our evaluation of the data, we examined fish habitat in two of the three study streams in summer 2011. Finally, we discuss the application of our findings to future experimental addition of large wood to increase the abundance and survival of juvenile salmonids.

MATERIALS AND METHODS

The three life cycle monitoring streams (LCMS) (Figure 1) were selected for a variety of reasons. Pudding Creek has a fish ladder where fish can be marked and released and has been operated as a LCMS by CTM since 2005. The South Fork Noyo River has coho salmon data relating to the Noyo Egg Collecting Station (ECS), fish can be captured and marked there, and it has been operated as an LCMS since 2000. Caspar Creek was chosen because of existing salmon monitoring data. In 2005 we built and operated a floating board resistance weir in Caspar Creek 4.9 km from the Pacific Ocean. To estimate escapement (Figure 2), we marked and released fish with weekly time-specific individually numbered bicolored floy tags (Szerlong and Rundio 2008). We estimated escapement using the Schnabel mark-recapture method (Krebs 1989) and conducted redd censuses in the three study streams following the methods of Gallagher and Knechtle (2003) and Gallagher et al. (2007). Over and under-counting errors in redd counts (bias corrected) were reduced following Gallagher and Gallagher (2005). Surveys were conducted approximately fortnightly from mid-November to late-April each year.

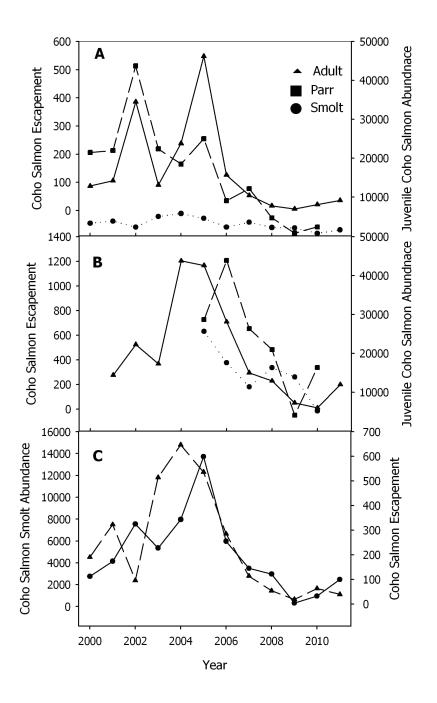


FIGURE 2.—Coho salmon abundance data for three life cycle monitoring streams, Mendocino County, California, 2000 to 2011. A. Caspar Creek; B. Pudding Creek; C. South Fork Noyo River.

We used downstream migrant traps to estimate smolt abundance using capturerecapture methods. Traps were placed in the streams in early March and checked daily until early June each year. We used a fyke trap, located about 5.0 km above the Pacific Ocean in the main stem of Caspar Creek, a screw trap below the ECS on the South Fork Noyo River (Figure 1), and a screw trap about 5 km upstream of the ocean in Pudding Creek. We installed two PIT tag antennae arrays about 0.5 km from the ocean in Caspar Creek and one array on the Pudding Creek dam during 2008. In 2010 we put another PIT tag antenna array in the fish ladder at Pudding Creek. We used PIT tags as the primary mark for fish >70 mm, and marked fish between 40 mm and 69 mm with site- and week-specific fin clips. We examined all trap-captured coho salmon for marks each day. Those without marks were marked and released at least 150 m above the traps and recaptured fish were released at least 150 m below the traps. We estimated smolt abundance using Darroch Analysis with Rank Reduction and a one-trap design (Bjorkstedt 2003). For coho salmon, we determined the following classes: <70 mm (YOY), 71-120 mm (Y+), and >120 mm (Y++) based on Shapovalov and Taft (1954), Gallagher (2000), and Neillands (2003).

Coho salmon parr abundance was estimated using depletion electro-fishing in earlyfall each year. In Caspar Creek, two 30-m sites have been sampled each fall since 1987 and an additional four sites were added in 1993 (B. Valentine, personal communication, March 2012). We used data collected at these sites to estimate parr abundance for 2000 to 2005. In 2006, we developed a 20-unit spatially balanced random sample draw of 50-m reaches in Pudding Creek for estimating summer rearing density. Similarly, but beginning in 2007, we randomly selected and sampled ten 50-m units in Caspar Creek. Salmonid density was estimated in each unit using depletion electro-fishing. All salmonids >60 mm fork length were given PIT tags and maxillary clips and all captured fish were examined for previously applied marks. We calculated the average and 95% CI density of salmonids by species in each stream and multiplied this by the total length of anadromy to estimate late-summer juvenile abundance.

We estimated annual coho egg to smolt, egg to parr, parr to smolt, and smolt to adult survival for the three streams from smolt abundance data from 2000 to 2011, from parr abundance data from 2006 to 2011 in Pudding Creek and 2000 to 2011 in Caspar Creek, and adult return data from 2000 through 2011. To estimate annual egg abundance we used the relationship between fecundity and fork length described by Shapovalov and Taft (1954), the average length of observed female coho salmon, and the estimated number of females in each stream each year. Over-winter survival was estimated for Caspar and Pudding creeks using data collected during summer electrofishing: summer stream-level population estimates were divided into smolt abundance estimates the following spring and the estimated number of summer PIT-tagged fish captured in downstream traps and detected in our arrays was divided by the total number of PIT tags deployed in summer.

We used key-factor analysis and calculated relative importance (RI) values following Guy and Brown (2007) from our estimates of relative marine (smolt to adult) and freshwater (egg to smolt, egg to parr, and parr to smolt) survival to determine which factor was more important in the observed variability in population abundance over our time series. Key-factor analysis is based on the idea that there is variation in survival at different life stages and variation in one life stage can affect abundance in later stages, with the most influential potentially driving overall population dynamics (Guy and Brown 2007). We also used the key-factor data to examine density dependence in the freshwater and marine environments by regressing each life stage k-value (k values = –log of stage specific

survival value) against the number of individuals entering that life stage. If the regression is statistically significant, density dependence is suspected (Guy and Brown 2007). For those instances in which we suspected density dependence, we fit our data to Beverton-Holt and Ricker spawner:recruit curves (Hilborn and Walters 1992, Guy and Brown 2007), evaluated potential carrying capacity, and related survival parameters.

Relationships between life-stage specific survival and readily available physical stream factors (flow, temperature, and turbidity) were examined graphically with scatter plots and statistically with correlation and regression. We used standardized coefficients to determine which of the independent variables (flow, temperature, or turbidity) had a greater effect on the dependent variable (survival) because the variables were measured in different units (Kim and Freree 1981). Because we suspected density dependence — and because freshwater survival was very high in 2009-10 indicating a release of the effects of density dependence on survival - we did not use data from this year in our correlation analysis. We obtained stream flow, water temperature, and turbidity data from 1999 to 2011 (the water temperature data series only covers 2005 to 2011) from the ongoing Caspar Creek watershed study (Cafferata et al. 2011). These data were collected continuously every 10 minutes at sediment weirs in the North Fork and South Fork of Caspar Creek (J. Seehafer, USFS, personal communication, November 2011) and we distilled it into seasonal (fall-September to November, winter-December to February, spring-March to May, summer-June to August) minimums, maximums, and averages. Only summer water temperature data were available for Pudding Creek. We estimated Pudding Creek seasonal stream flows as one-sixth of the Noyo River based on our knowledge of the two systems.

We used the habitat classification of Bouwes et al. (2011) to conduct summer habitat censuses in Caspar and Pudding creeks in 2011. We evaluated eight physical habitat factors collected during habitat censuses conducted in each stream (unit type, unit length, unit width, unit area, unit volume, substrate, percent fish cover, and large wood density; Bouwes et al. 2011). Habitat variables were compared using chi-square tests, *t*-tests, or Mann-Whitney tests when standard kurtosis *P*-values were significantly different from zero. Because our work involved endangered species (Good et al. 2005), we accepted statistical significance at P < 0.10.

RESULTS

Between 2000 and 2003, marine survival averaged around 7%, dropped to average <1% between 2005 and 2008, and increased to about 5% in 2009 in the three study streams. During this same period freshwater (egg to smolt) survival averaged approximately 3% from 2000 to 2003 and increased as marine survival dropped (Figure 3a). During the low adult return years of 2009 and 2010, (Figure 2) freshwater survival increased dramatically (Figure 3), indicating a release from density dependence. Coho salmon over-winter and over-summer survival was very similar between 2000 and 2007, after which over-winter survival appeared to account for the overall increase in egg to smolt survival (Figure 3b, c).

For coho salmon it appears that marine survival was more influential in the observed variability in population abundance over our time series than was freshwater survival. Key-factor analysis showed that marine survival more closely tracked variation in total survival than did freshwater survival (Figure 4) for all three streams. Marine survival was relatively more important than freshwater survival for the South Fork Noyo River population (RI = 0.81 versus 0.19), for the Caspar Creek population (RI = 0.70 versus 0.30), and for the Pudding Creek population (RI = 0.99 versus 0.01).

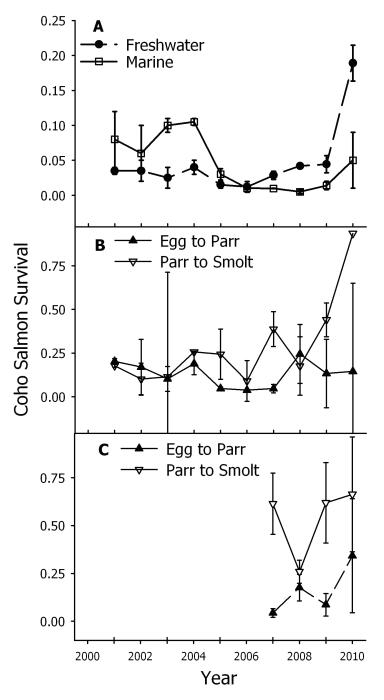


FIGURE 3.—Coho salmon survival for three coastal Mendocino County, California, streams 2000 to 2010. A. Three stream average freshwater and marine survival; B. Caspar Creek freshwater survival; C. Pudding Creek freshwater survival.

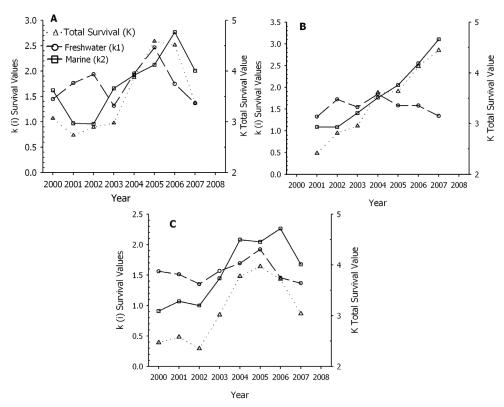


FIGURE 4.—Key-factor survival analysis for coho salmon in three streams in coastal Mendocino County, California. A. Caspar Creek; B. Pudding Creek; C. South Fork Noyo River.

Our k-value versus life stage abundance analysis indicated density dependence in freshwater, but not in the marine environment (Figure 5); this pattern was the same in all three streams. Regressions of freshwater life stage k-values against the number of eggs estimated in each stream were statistically significant (Figure 5a, c, e). However, marine k-values versus smolt abundance regressions were not significant (Figure 5b, d, f).

We fit our smolt and egg data to Beverton-Holt and Ricker recruitment functions and examined the resulting graphs to help identify carrying capacity (Figure 6). Pudding Creek appeared to be the most productive and had a smolt carrying capacity of around 20,000. Caspar Creek appeared to have a carrying capacity of about 4,500 smolts, and the South Fork Noyo River asymptotes at about 8,000 smolts. Pudding Creek produced on average 948 smolts/km, Caspar Creek produced on average 216 smolts/km, and the South Fork Noyo River produced an average of 203 smolts/km of stream.

Average winter stream flow was negatively correlated with coho salmon parr to smolt survival in both Caspar (r = -0.67, P = 0.047) and Pudding Creeks (r = -0.96, p = 0.17). Maximum winter stream flow was negatively correlated with coho salmon parr to smolt survival in both Caspar (r = -0.77, P = 0.02) and Pudding Creeks (r = -0.99, P = 0.09). Egg to parr survival was negatively correlated with first winter average water temperature

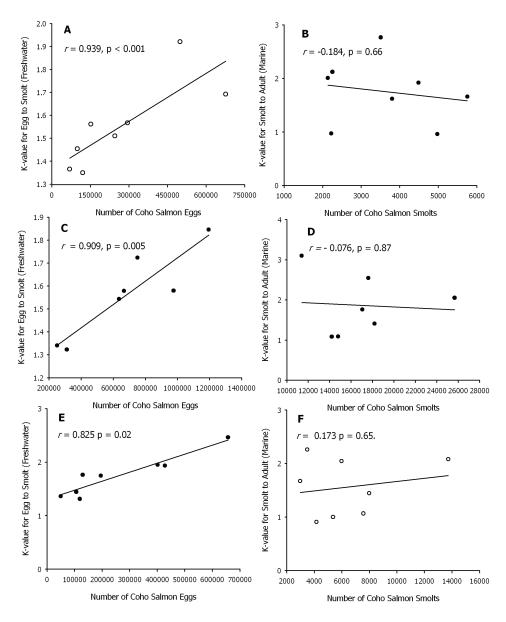


FIGURE 5.—Regression of coho salmon freshwater survival k-values against egg production (A, C, E) and marine survival k-values versus smolt abundance (B, D, F) in three streams in coastal Mendocino County, California. A-B. Caspar Creek; C-D. Pudding Creek; E-F. South Fork Noyo River. Significant relationships suggest density dependence.

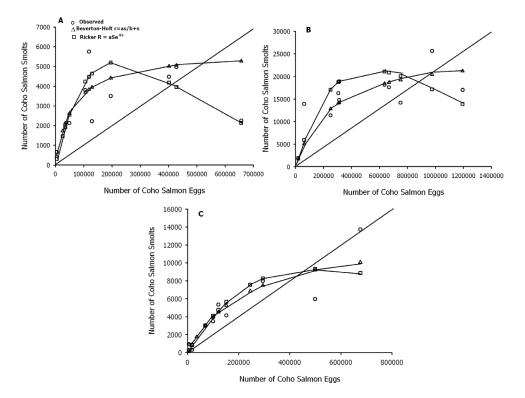


FIGURE 6.—Coho salmon egg to smolt recruitment curves for three streams in coastal Mendocino County, California. A. Caspar Creek; B. Pudding Creek; C. South Fork Noyo River. The horizontal line indicates 1:1 replacement.

(r = -0.85, P = 0.07) in Caspar Creek. Parr to smolt survival was also negatively associated with second winter average water temperature (r = -0.90, P = 0.04), second winter average turbidity (r = -0.62, P = 0.08), and second spring minimum turbidity (r = -0.63, P = 0.07) in Caspar Creek. In Pudding Creek, parr to smolt survival was positively associated with fall average (r = 0.99, P = 0.02), second spring minimum (r = 1.0, P = 0.01), and second spring maximum stream flows (r = 0.99, P = 0.02). We suspect the three later correlations in Pudding Creek were an artifact of small sample size, because, on further inspection, there was a similar pattern of a negative association between parr to smolt survival and both winter average and winter maximum flows during the three years data are available for both streams (Figure 7a, b). An opposing pattern emerged for minimum and maximum flows in those streams during spring (Figure 7c, d). With only three years of data we could thus erroneously conclude that these flows were associated with survival (the pattern was the same for average fall flows; data not presented). None of the other relationships we tested between survival and seasonal stream flows, water temperatures, or turbidity were significant in either stream.

Caspar Creek stream flows were positively correlated with both water temperature (r=0.43, P<0.001) and turbidity (r=0.91, P<0.001). The standardized coefficients showed that the order of influence of the three physical variables on coho salmon part to smolt

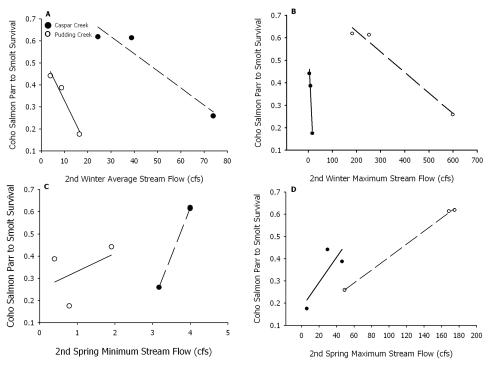


FIGURE 7.— Coho salmon parr to smolt survival and stream flow in Caspar and Pudding creeks, Mendocino County, California. A. second winter average; B. second winter maximum; C. second spring minimum; D. second spring maximum.

survival was (1) stream flow (Beta = -0.94); (2) water temperature (Beta = 0.82); and, (3) turbidity (Beta = -0.22).

Summer 2011 Habitat Evaluations.—The frequency of habitat units was not significantly different between Caspar and Pudding creeks ($X_{30}^2 = 34.7, P = 0.25$); however, Caspar Creek had a higher percentage of pools than did Pudding Creek (55.8% versus 39.4%). The surface area of habitat in each stream was not significantly different ($U = 7635, n_1 = 83, n_2 = 109, P = 0.33$); however, Pudding Creek had more length of stream habitat above the dam pond (17.1 km) than Caspar Creek (14.1 km), and about 1.36 km more pool habitat than the latter. Total habitat volume was not significantly different between the two streams ($U = 7480, n_1 = 83, n_2 = 109, P = 0.17$). Fish cover (percent wood, vegetation, and undercut) was not significantly different between these streams ($U > 7717, n_1 = 83, n_2 = 109, P > 0.24$). Large wood density was not significantly different between Caspar and Pudding creeks ($U = 8192, n_1 = 83, n_2 = 109, P = 0.63$). Caspar and Pudding creeks had similar bank full widths ($U = 7922, n_1 = 83, n_2 = 109, P = 0.94$). Caspar Creek had significantly more large cobble cover (average 8.6% SE = 1.4%) than did Pudding Creek (3.4% SE = 0.94%) ($U = 9458, n_1 = 83, n_2 = 109, P = 0.001$). Pudding Creek had more (16.7%) fine sediment than did Caspar Creek (14.1% SE = 2.5%) ($U = 6955, n_1 = 83, n_2 = 109, P = 0.02$).

When examined by habitat unit, Pudding Creek had significantly deeper pools than Caspar Creek did (0.77 m, SE = 0.05 versus 0.63 m, SE = 0.05). Maximum pool depth (t = -2.07, df = 77, P = 0.04), residual pool depth (U = 1214, $n_1 = 38$, $n_2 = 43$, P = 0.03), and

pool volume (U = 1352, $n_1 = 38$, $n_2 = 43$, P = 0.05) were significantly different between the two creeks. While Pudding Creek only has about 4% more habitat overall, it had twice the pool volume of Caspar Creek (14,869 m³ versus 7,862 m³). Riffles in Pudding Creek had a significantly lower percentage of cobbles (3.3% versus 7.6%; U = 638, $n_1 = 19$, $n_2 = 33$, P = 0.01) and a significantly higher percentage of fines (8.1% versus 3.7%; U = 387, $n_1 = 38$, $n_2 = 43$, P = 0.03) than Caspar Creek. Pools had a higher percentage of cobble in Caspar Creek than Pudding did (7.5% versus 3.9%; U = 1906, $n_1 = 38$, $n_2 = 43$, P = 0.005). Importantly, large wood density (U > 565, $n_1 = 83$, $n_2 = 109$, P > 0.11) and percentage of fish cover provided by large wood (U > 596, $n_1 = 83$, $n_2 = 109$, P > 0.46) was not significantly different in any habitat type between the streams. In both streams the percentage of fish cover provided by wood, undercut banks, and vegetation was <25% of the stream surface area.

DISCUSSION

Coho salmon smolt and adult abundances trends were very similar among the three streams over the past 11 years. Parr abundance trends also appeared to track well over the shorter time series in Caspar and Pudding creeks (Figure 2). Coho salmon freshwater and marine survival were also very similar over the time series and tracked well among the three streams (Figure 3). The relationships we observed between survival and high winter stream flow were the same in Caspar and Pudding creeks. The patterns we observed in the importance of freshwater and marine survival were virtually the same in the two study streams (Figure 4) and all three streams showed density dependence in freshwater but not in the marine environment (Figure 5).

Coho smolt to adult survival over nine smolt-to-adult return cycles was similar to that reported by Bradford (1999), Logerwell et al. (2003), and Shapovolov and Taft (1954) between 2002 and 2005, was considerably lower from 2006 to 2010, and appears to have increased some in 2011. Coho salmon egg to smolt survival (freshwater) ranged from 1% to over 20% over the last 10 years and was very similar among the three streams. Coho smolt to adult (marine) survival was similar among streams over 10 years and ranged from 0.002 to 0.17.

It appears that conditions in the marine environment have a greater influence on overall survival relative to freshwater. However, our key-factor analysis suggests there is density dependence (e.g., carrying capacity, competition, favorable habitat) in the freshwater phase of the coho salmon's life cycle, but there is no evidence for density dependence in the marine environment. We suspect the large increase in freshwater survival observed between 2009 and 2010 (Figure 3) provides further support for the idea that coho salmon experience density dependence in freshwater. Because adult returns in 2009 (Figure 2) were very low, there were very few young salmon produced into relatively large areas of habitat. Moore et al. (2011) showed that coho salmon smolts were larger and disproportionately more abundant at lower spawner abundances, and attributed this to density dependence. Thus, we expect that if we create effective restorations to improve coho salmon and steelhead freshwater survival and abundance that, even in times of poor ocean conditions, more fish will survive to return as adults because freshwater is crucial to providing stock resilience to fluctuations in the marine environment.

Pudding Creek produced over four times as many smolts as Caspar Creek and the South Fork Noyo River, and had a carrying capacity three to five times greater than the other two streams. While Pudding and Caspar creeks had similar proportions of habitats, Pudding Creek had significantly deeper pools and twice the pool volume, which may explain why it was more productive. The difference in average depth between the two streams was only about 0.10 m. While not significantly steeper, Caspar Creek had a higher gradient (0.15%) than did Pudding Creek (0.08%), which may explain why it had deeper pools in summer. Further investigation of factors influencing the productivity of these streams in winter will help direct habitat restoration. Our estimates of carrying capacity in the three streams will also serve as a baseline for monitoring the effects of restoration.

It was surprising that summer low flows, summer high temperatures, and that many of the other seasonal physical variables we examined were not related to coho salmon freshwater survival. High flows in fall can be beneficial to fish because it is the period of the lowest steam flows and thus the highest relative fish density. Higher fall stream flows could result in more habitat space and the potential lessening of some density dependent pressures. Similarly, high flows in spring might be beneficial for predator avoidance and aiding smolt migrations. Low turbidity in spring may negatively influence survival by increasing predation. We observed significant positive associations between survival and fall and spring flows in Pudding Creek, with only three years of data. In Caspar Creek, with a longer time series, however, we did not detect the same relationships; therefore, we attribute the Pudding Creek observations to small sample size. Our analysis of coho salmon seasonal growth (Wright et al. 2012) indicated that summer is a low growth period, and we expected to see a relationship between survival and summer low flow or high temperatures. That both egg to parr and parr to smolt survival was negatively associated with water temperature is worrisome, given the potential for continued increase in temperature because of climate change. Lawson et al. (2004) reported a strong negative relationship between smolt production and temperature.

Our analysis of freshwater survival and seasonal stream flows, temperatures, and turbidity indicates that a lack of winter slow-water habitat is limiting coho salmon production in Caspar and Pudding creeks. Coho salmon parr to smolt survival was negatively correlated with winter average and high stream flows in both creeks. Survival for this life stage was also negatively correlated with elevated winter water temperatures and turbidity in Caspar Creek, and the standardized coefficient analysis showed that high stream flow was the main driver. Our results add to existing evidence to support the idea that winter high flows limit coho salmon survival. Nickelson et al. (1992) reasoned that since coho fry and juveniles were most abundant in alcoves and beaver ponds in winter, and because these habitats were rare, winter habitat probably limited coho salmon production in coastal Oregon streams. Using a before-after-control-impact design (BACI; Stewart-Oaten 1986) and large wood treatments, Solazzi et al. (2000) reported that winter habitat was limiting for coho salmon and steelhead in Oregon. Johnson et al. (2005) reported that coho salmon and steelhead freshwater survival increased after the input of large wood in a coastal Oregon stream. We have directly demonstrated, by evaluating life stage specific survival and seasonal flows, that a paucity of suitable winter habitat likely limits coho production in streams in coastal California.

Following a major literature review, Mellina and Hinch (2009) concluded that large wood removal has a negative effect on juvenile salmonids. Wood in rivers is important in many ways, such as a source of food for invertebrates, habitat for vertebrates, and dissipating energy by scouring channels (Maser and Sedell 1994). Both Caspar and Pudding creeks experienced substantial removals of large wood during the stream cleaning in the 1970s and

1980s (A. Grass, CDFG, personal communication, June 2008). Our census of habitat types and large wood in both study streams found no difference in large wood density, and that total fish cover was <25%. Pools in Caspar Creek averaged 0.24 large wood pieces/m (95% CI = 0.09 – 0.40) and in Pudding Creek averaged 0.32 pieces/m (95% CI = 0.10-0.54). We believe these values are low for salmon streams. In 2006, Pudding Creek had mean shelter (fish cover, primarily large wood) values of 41 for pools and 11 for flat-water habitats (CDFG 2006a) and Caspar Creek had a shelter rating of 82 for pools and 36 for flat-water habitats (CDFG 2006b). A value of 100 is considered the minimum required level of shelter (Flosi et al. 1998). Both NOAA (2010) and CDFG (2004) suggest, in addition to improving water quality and other watershed functions, large wood is needed to help recover listed coho salmon because it will induce sediment sorting, improve habitat shelter, increase pool frequency and depth, and reconnect flood plains.

The proportion and surface area of habitat units in summer 2011 were not statistically different between Caspar and Pudding creeks. Additionally, there were few differences in physical habitat between Caspar and Pudding creeks; both streams had low instream densities of large wood and lacked fish cover. Because Caspar and Pudding creeks have similar habitat characteristics, and since all the biological metrics varied similarly among these streams over our time series, they would be good choices for experimentally evaluating fish responses to stream habitat restoration in a BACI experiment (J. Ferreira, CDFG, personal communication, February 2012). Johnson et al. (2005) reported that their reference stream was a poor choice because salmonid abundance did not track in the treatment stream, which violates the assumptions of the BACI analysis (Stewart-Oten 1986).

Our data analyses and literature review point to winter habitat as limiting coho salmon, and we think that adding substantial amounts of large wood will, through stream action, increase pool habitats, improve stream shelter, and reconnect the stream to flood plain habitats, with a resultant increase in coho salmon survival and abundance. Future work should consider a BACI experiment to test the hypothesis that strategically and surgically placing large wood into most of the suitable salmonid habitat in Pudding Creek will enhance coho salmon and steelhead growth, survival, and abundance by increasing availability of summer and winter habitat relative to Caspar Creek as a control.

ACKNOWLEDGMENTS

This work was funded by the California Department of Fish and Game Fisheries Restoration Grant Program (Grants P0410527, P0510544, P0610540, P0710540, and P0810312). Research on live fish followed appropriate guidelines required under the Endangered Species Act Section 10 process (Permit number 10093) and CDFG policies. Many individuals, too numerous to mention by name, from CDFG, CTM, NOAA Fisheries Santa Cruz, and the Pacific States Marine Fisheries Commission helped with this study; be assured we value your help. A few we are compelled to mention specifically include S. Allen for administrative support, W. Holloway for help with Figure 1, E. Lang, and C. Bell for many long hours in the field, and C. Gallagher and J. Ferreira for statistical assistance. D. Albin, V. Bleich, L. Bolton, S. Hayes, D. Porter, K. Shaffer, and an anonymous reviewer provided useful comments that greatly improved the manuscript.

LITERATURE CITED

- ADAMS, P. B., L. B. BOYDSTUN, S. P. GALLAGHER, M. K. LACY, T. MCDONALD, AND K. E. SHAFFER. 2011. California coastal salmonid population monitoring: strategy, design, and methods. California Department of Fish and Game Fish Bulletin 180.
- BERNHARDT, E. S., AND 24 OTHERS. 2005. Synthesizing U.S. river restoration efforts. Science 308:636-637.
- BJORKSTEDT, E. P. 2003. DARR (Darroch analysis with rank-reduction) a method for analysis of stratified mark-recapture data for small populations, with application to estimating abundance of smolts from out-migrant trap data. Administrative Report SC-00-02. National Marine Fisheries Service, Southwest Fisheries Science Center, Santa Cruz, California, USA.
- BOUWES, N., J. MOBERG, N. WEBER, B. BOUWES, C. BEASLY, S. BENNETT, A. HILL, C. JORDAN, R. MILLER, P. NELLE, M. POLINO, S. RENTMEESTER, B. SEMMENS, C. VOLK, M. B. WARD, G. WATHEN, AND J. WHITE. 2011. Scientific protocol for salmonid habitat surveys within the Columbia Habitat Monitoring Program. Terraqua, Inc., Wauconda, Washington, USA.
- BRADFORD, M. J. 1999. Temporal and spatial trends in the abundance of coho salmon smolts from western North America. Transactions of the American Fisheries Society 128:840-846.
- CAFFERATA, P. H., AND L. M. REID. 2011. Applications of long-term watershed research to forest management in California: 50 years of learning from the Caspar Creek watershed study. Proceedings of coast redwood forests in a changing California: a symposium for scientists and managers. General Technical Report PSW-GTR-238. Pacific Southwest Research Station, Albany, California, USA.
- CDFG (CALIFORNIA DEPARTMENT OF FISH AND GAME). 2006a. Stream inventory report, Pudding Creek. California Department of Fish and Game, Inland Fisheries Division, Fortuna, USA.
- CDFG (CALIFORNIA DEPARTMENT OF FISH AND GAME). 2006b. Stream inventory report, Caspar Creek. California Department of Fish and Game, Inland Fisheries Division, Fortuna, USA.
- CDFG (CALIFORNIA DEPARTMENT OF FISH AND GAME). 2004. Recovery strategy for California coho salmon. Report to the California Fish and Game Commission. California Department of Fish and Game, Native Anadromous Fish and Watershed Branch, Sacramento, USA.
- FLOSI, G., S. DOWNIE, J. HOPELAIN, M. BIRD, R. COEY, AND B. COLLINS. 1998. California salmonid stream habitat restoration manual. Third edition. California Department of Fish and Game, Inland Fisheries Division, Fortuna, USA.
- GALLAGHER, S. P. 2000. Results of the 2000 Steelhead (*Oncorhynchus mykiss*) Fyke trapping and stream resident population estimations and predictions for the Noyo River, California with comparison to some historic information. Report FB-03. California Department of Fish and Game, Fort Bragg, California, USA.
- GALLAGHER, S. P., AND C. M. GALLAGHER. 2005. Discrimination of Chinook and coho salmon and steelhead redds and evaluation of the use of redd data for estimating escapement in several unregulated streams in northern California. North American Journal of Fisheries Management 25:284-300.

- GALLAGHER, S. P., AND M. KNECHTLE. 2003. Coastal northern California salmonid spawning survey protocol. California Department of Fish and Game, Fort Bragg, USA.
- GALLAGHER, S. P., P. K. HAHN, AND D. H. JOHNSON. 2007. Redd counts. Pages 197-234 in D. H. Johnson, B. M. Shrier, J. S. O'Neal, J. A. Knutzen, X. Augerot, T. A. O'Neil, and T. N. Pearsons, editors. Salmonid field protocols handbook: techniques for assessing status and trends in salmon and trout populations. American Fisheries Society, Bethesda, Maryland, USA.
- GOOD, T. P., R. S. WAPLES, AND P. ADAMS (EDITORS). 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. Administrative Report NMFS-NWFSC-66. National Marine Fisheries Service, Southwest Fisheries Science Center, Santa Cruz, California, USA.
- GUY, C. S., AND M. L. BROWN (EDITORS). 2007. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland, USA.
- HILBORN, R., AND C. J. WALTERS. 1992. Quantitative fisheries stock assessments: choice, dynamics, and uncertainty. Chapman and Hall, New York, USA.
- JOHNSON, S. L., J. D. RODGERS, M. F. SOLAZZI, AND T. E. NICKELSON. 2005. Effects of an increase in large wood on abundance and survival of juvenile salmonids (*Oncorhynchus sp.*) in an Oregon coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 62:412-424.
- KIM, J., AND G. FEREE. 1981. Standardization in causal analysis. Sociological Methods and Research 10:187-210.
- KREBS, C. J. 1989. Ecological methodology. Harper and Row, New York, USA.
- LAWSON, P. W., E. A. LOGERWELL, N. J. MANTUA, R. C. FRANCIS, AND V. N. AGOSTINI. 2004. Environmental factors influencing freshwater survival and smolt production in Pacific Northwest coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 61:360-373.
- LOGERWELL, E. A., N. MANTUA, P. W. LAWSON, R. C. FRANCIS, AND V. N. AGOSTINI. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fisheries Oceanography 12:554-568.
- MASER, C., AND J. R. SEDELL. 1994. From the forest to the sea: the ecology of wood in streams, rivers, estuaries, oceans. St. Lucie Press, Minneapolis, Minnesota, USA.
- MELLINA, E., AND S. G. HITCH. 2009. Influences of riparian logging and in-stream large wood removal on pool habitat and salmonid density and biomass: a meta-analysis. Canadian Journal of Forestry Research 39:1280-1301.
- MOORE, J. W., S. A. HAYES, W. DUFFY, S. P. GALLAGHER, C. MICHEL, AND D. WRIGHT. 2011. Nutrient fluxes and the recent collapse of coastal California salmon populations. Canadian Journal of Fisheries and Aquatic Sciences 68:1161-1170.
- NOAA (NATIONAL MARINE FISHERIES SERVICE). 2010. Public draft recovery plan for central California coast coho salmon (*Oncorhynchus kisutch*) evolutionarily significant unit. National Marine Fisheries Service, Southwest Region, Santa Rosa, California, USA.
- NOAA (NATIONAL MARINE FISHERIES SERVICE). 2012. Public draft recovery plan for southern Oregon Northern California coast coho salmon (*Oncorhynchus kisutch*) evolutionarily significant unit. National Marine Fisheries Service, Southwest Region, Arcata, California, USA.

- NICKELSON, E. E., J. D. RODGERS, S. L. JOHNSON, AND M. F. SOLAZZI. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49:783-789.
- NEILLANDS, W. G. 2003. Northern California steelhead (*Oncorhynchus mykiss*) life history diversity analysis, 2001-2002 annual report. California Department of Fish and Game, Coastal Watershed Planning and Assessment Program, Fortuna, USA.
- RONI, P., K. HANSON, AND T. BEECHIE. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. North American Journal of Fisheries Management 28:856-890.
- RONI, P., G. PESS, T. BEECHIE, AND S. MORELY. 2010. Estimating changes in coho salmon and steelhead abundance from watershed restoration: how much restoration is needed to measurably increase smolt production? North American Journal of Fisheries Management 30:1469-1484.
- SHAPOVALOV, L., AND A. C. TAFT. 1954. The life histories of the steelhead rainbow trout (Salmo gairdneri) and silver salmon (Oncorhynchus kisutch) with special reference to Waddell Creek, California and recommendations regarding their management. California Department of Fish and Game Fish Bulletin 98.
- SOLAZZI, M. F., T. E. NICKELSON, S. L. JOHNSON, AND J. D. RODGERS. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 57:900-914.
- STEWART-OATEN, A., W. W. MURDOCH, AND K. R. PARKER. 1986. Environmental impact assessment: "psuedoreplication" in time? Ecology 67:929-940.
- SZERLONG, R. G., AND D. E. RUNDIO. 2008. A statistical modeling method for estimating mortality and abundance of spawning salmon from a time series of counts. Canadian Journal of Fisheries and Aquatic Sciences 65:17-26.
- WRIGHT, D. W., S. P. GALLAGHER, AND C. J. HANNON. 2012. Measurement of key life history metrics of coho salmon in Pudding Creek, California. Pages 459-470 in R. B. Standiford, T. J. Weller, D. D. Piirto, and J. D. Stuart, technical coordinators. Proceedings of coast redwood forests in a changing California: a symposium for scientists and managers. General Technical Report PSW-GTR-238. Pacific Southwest Research Station, Albany, California, USA.

Received 7 June 2012 Accepted 21 September 2012 Associate Editor was K. Shaffer